Maturation and Repeat Spawning by American Shad in the York River, Virginia

Kristin L. Maki

College of William and Mary - Virginia Institute of Marine Science

Follow this and additional works at: https://scholarworks.wm.edu/etd

Part of the Fresh Water Studies Commons, Oceanography Commons, and the Zoology Commons

Recommended Citation
https://dx.doi.org/doi:10.25773/v5-g28h-sd53

This Thesis is brought to you for free and open access by the Theses, Dissertations, & Master Projects at W&M ScholarWorks. It has been accepted for inclusion in Dissertations, Theses, and Masters Projects by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.
MATURATION AND REPEAT SPAWNING BY AMERICAN SHAD
IN THE YORK RIVER, VIRGINIA

A Thesis
Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

by
Kristin L. Maki
2000
This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

Kristin L. Maki

Approved December, 2000

John E. Olney, Ph.D.
Committee Chairman/Advisor

John M. Hoenig, Ph.D.

Peter Van Veld, Ph.D.

David H. Secor, Ph.D.
Chesapeake Biological Laboratory
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vii</td>
</tr>
<tr>
<td>CHAPTER 1. GENERAL INTRODUCTION</td>
<td>2</td>
</tr>
<tr>
<td>CHAPTER 2. ESTIMATING PROPORTION MATURE AT AGE WHEN IMMATURE FISH ARE UNAVAILABLE FOR STUDY, WITH APPLICATION TO AMERICAN SHAD IN THE YORK RIVER, VIRGINIA</td>
<td>8</td>
</tr>
<tr>
<td>CHAPTER 3. INTERPRETING MATURATION DATA FOR AMERICAN SHAD IN THE PRESENCE OF FISHING MORTALITY - A LOOK AT HISTORICAL DATA FROM THE YORK RIVER, VIRGINIA</td>
<td>46</td>
</tr>
<tr>
<td>THESIS BIBLIOGRAPHY</td>
<td>67</td>
</tr>
<tr>
<td>APPENDIX A: RESIDUALS FROM THE MAXIMUM LIKELIHOOD ESTIMATION OF PROPORTIONS OF SHAD MATURING</td>
<td>71</td>
</tr>
<tr>
<td>APPENDIX B: ANALYSIS OF EQUAL CATCHABILITY BETWEEN EARLY AND LATE MATURING SHAD OF A GIVEN AGE</td>
<td>75</td>
</tr>
<tr>
<td>APPENDIX C: C++ CODE FOR RECONSTRUCTION OF DATA TABLES WHEN COLUMN, ROW, AND DIAGONAL SUMS ARE KNOWN</td>
<td>77</td>
</tr>
<tr>
<td>VITA</td>
<td>87</td>
</tr>
</tbody>
</table>

iii
ACKNOWLEDGMENTS

I would like to thank my major advisor, John Olney, Sr., for his guidance and support throughout this project. Even when the light seemed dim at the end of the tunnel, John’s faith in my abilities never wavered.

I would like to thank John Hoenig for the valuable time he spent with me at the chalkboard easing me into the world of maximum likelihood estimation. Without his patience and dedication, this project would not have been feasible.

I would also like to acknowledge the remaining members of my committee, Pete Van Veld and David Secor, for helpful comments and essential suggestions throughout this project. Dave, thank you for sticking with me even when I (momentarily) abandoned the world of otoliths.

Thank you to the many members of the Anadromous Fishes Research program who worked many long, tiresome, and often very cold, hours collecting and processing the numerous shad samples utilized by this project. I’d like to thank John Walter and Mary Lynn (Aiken) Wilhite for providing, in addition to friendship and encouragement, valuable insight into the realm of shad.

I am grateful to the numerous individuals who assisted me at various stages of this project: Raymond and Tony Kellum for their assistance in the field. Dennis Heisey for suggesting the analytical procedure for obtaining the maximum likelihood estimates, Daniel Hepworth for his ingenious S-plus programming abilities, Kathy Hattala for assistance in interpreting scales, Alex Hoenig for writing the C++ program to reconstruct data tables, and Patti Marraro and Joseph Smith who helped me obtain historical raw data.

Finally, none of this would have been possible without the continual love and support from friends and family. To my friends, both near and far, thank you for always being there to listen to me complain, provide me with advice, and not avoid me when I smelled like fish! I would like to thank my family for their generous support and love that has not diminished since the day I was born, through good times and bad. Without you I would not have had the courage to make the decisions that have led me down this road. I love you all.
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CHAPTER 2</strong></td>
<td></td>
</tr>
<tr>
<td><strong>CHAPTER 3</strong></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Spawning histories of American shad collected in the York River during 1998, 1999, and 2000</td>
</tr>
<tr>
<td>2</td>
<td>Published and revised catch and spawning data for 1959</td>
</tr>
<tr>
<td>3</td>
<td>Estimates of conditional maturation at age parameters for current and 1959 data</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-1</td>
<td>True versus estimated fraction maturing at age for values of R</td>
<td>36</td>
</tr>
<tr>
<td>B-2</td>
<td>True versus estimated proportion mature by age for values of R</td>
<td>37</td>
</tr>
<tr>
<td>B-3</td>
<td>Estimates of the conditional maturity parameters for values of R</td>
<td>38</td>
</tr>
<tr>
<td>1</td>
<td>Residuals of the maximum likelihood model</td>
<td>41</td>
</tr>
<tr>
<td>2</td>
<td>Proportion maturing by age for combined data set.</td>
<td>42</td>
</tr>
<tr>
<td>3</td>
<td>Confidence intervals representing proportion mature by age for 1998, 1999, and 2000</td>
<td>43</td>
</tr>
<tr>
<td>4</td>
<td>Maximum likelihood estimates versus sample proportion estimates</td>
<td>44</td>
</tr>
<tr>
<td>5</td>
<td>Testing for equal catchability of early and late maturing shad</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APPENDIX A</td>
<td>Residuals of the maximum likelihood model for 1998</td>
<td>72</td>
</tr>
<tr>
<td>A-2</td>
<td>Residuals of the maximum likelihood model for 1999</td>
<td>73</td>
</tr>
<tr>
<td>A-3</td>
<td>Residuals of the maximum likelihood model for 2000</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APPENDIX B</td>
<td>Testing for equal catchability of early and late maturing shad</td>
<td>76</td>
</tr>
</tbody>
</table>
ABSTRACT

A model is developed 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 is used to estimate the probabilities of shad maturing at given ages. Shad collected in the York River during 1998, 1999, and 2000 matured between the ages of three and seven. Maturity schedules are estimated for each of these years, as well as for the three-year combined data set by cumulating the maximum likelihood estimates and are found to generally overlap for the three years of data. However, the model is sensitive to differential survival between immature and mature fish of the same age. A historical data source was identified as containing the data necessary to allow reconstruction of maturation schedules from historical periods of commercial fishing and enable comparison with the recent maturation schedules. However, since during times of commercial fishing, mature survival likely does not equal immature survival for a given age, development of a maturity model that can account for the relationship between mature and immature survival is required and is developed here. A process for reconstructing data matrices from the published data summaries is developed, resulting in the discovery of errors in the historical data source. For the year in which the errors can be corrected, maturation parameters are estimated using the method developed here for various levels of the ratio of mature to immature survival. It is concluded that either shad matured earlier during this historic time period or that the estimated exploitation rate given in the data source is too high. The developed model is also appropriate for use in contemporary times for populations of shad which are currently subjected to in-river commercial fishing (and thus mature survival is likely different from immature survival for shad of a given age).
MATURATION AND REPEAT SPAWNING BY AMERICAN SHAD IN THE YORK RIVER, VIRGINIA
The American shad (*Alosa sapidissima*) is the largest clupeid in North America. It is an anadromous species, spending most of its life in the sea and ascending coastal freshwater rivers to spawn. American shad are native to the Atlantic coast, ranging from the St. Johns River, Florida to the St. Lawrence River, Canada, and are most abundant from Connecticut to North Carolina (Walburg and Nichols, 1967). Populations of American shad also occur on the Pacific coast of North America, ranging from the Mexican border to Cook Inlet, Alaska, following introductions into the Sacramento and Columbia Rivers (Neave, 1954; Walburg and Nichols, 1967). Description of American shad life history is limited to Atlantic coast populations for the purposes of this study.

Juvenile shad migrate downriver as a function of age and size-at-age, with all juveniles exiting the natal stream by late fall (Limburg, 1996). Shad remain in the ocean until they reach sexual maturity (3 to 7 years for York River shad, Maki et al., in review). American shad are long-distance coastal migrants and most sexually mature fish return to the streams of their birth to spawn (Talbot and Sykes, 1958; Walburg, 1960; Carscadden and Leggett, 1975; Melvin et al. 1986).

American shad begin the spawning migration into freshwater earliest in the southern regions of its range (Talbot and Sykes, 1958). Spawning begins as early as
December in Florida (Williams and Bruger, 1972) and continues progressively northward, occurring as late as early July in the St. Lawrence River, Quebec (Vladykov, 1950 in Melvin et al., 1986). Time of spawning has been attributed primarily to temperature (Massmann and Pacheco, 1957; Walburg, 1960; Leggett and Whitney, 1972; Melvin et al., 1986). Shad that survive fishing during the spawning migration and do not die after spawning (as is presumed to be the case with some southern populations) return to sea. The following year they again return to freshwater to spawn and are termed "repeaters" (Talbot and Sykes, 1958).

The American shad was historically one of the most important anadromous fishes in the United States. During the 19th century, shad fisheries developed to great importance along the Atlantic coast of the United States and supported commercial fishing in every coastal state (Walburg and Nichols, 1967). Since the late 1800's, however, there has been a steady decline in the abundance of American shad along the Atlantic coast. In 1896, the yield of American shad was more than 50 million pounds valued in excess of $1.6 million. Catch in 1908 was slightly less than 25 million pounds valued at more than $2 million (Walburg and Nichols, 1967). By 1980, however, the landings had decreased dramatically to 3.8 million pounds, and by 1993, only 1.5 million pounds were landed (Atlantic States Marine Fisheries Commission, 1999). This decline in landings has been attributed to several factors including overfishing, construction of dams, and pollution (Winslow, 1990).

The large declines in commercial landings of American shad (as well as hickory shad, alewife, and blueback herring) prompted the Atlantic States Marine Fisheries
Commission (ASMFC) to recommend the preparation of a cooperative Interstate Fishery Management Plan for American shad and river herrings. The plan was completed in 1985 and a supplement approved in 1988. The plan specified recommended management measures, focused primarily on regulating exploitation and enhancing stock restoration efforts. However, the plan did not require any specific management approach or monitoring programs within the management unit and asked only that states provide annual summaries of restoration efforts and ocean fishery activity. In 1994, the Plan Review Team and the Management Board determined that the original 1985 plan was no longer adequate for protecting or restoring the remaining shad and river herring stocks (ASMFC, 1999).

In October of 1998, the ASMFC adopted Amendment I to the Interstate Fishery Management Plan for Shad & River Herring which provides management guidance by setting specific standards to be met by the states. Under this amendment, states are required to implement various surveys including adult spawning stock surveys. As part of these surveys, states are "required to take representative samples of adults to determine sex and age composition, repeat spawning (for states north of South Carolina), and size distribution of each stock within their jurisdiction" (ASMFC, 1999).

This analysis of shad maturation in the York River was prompted by the need to develop monitoring, forecasting, and restoration plans for American shad in Virginia’s waters. Maturation data is useful for forecasting when the effects of an especially strong or weak year class appear in juvenile monitoring and for predicting subsequent adult spawning runs from current run data. Thus, it is not only necessary to gain an
understanding of current maturation patterns, but also to know if maturation rates change appreciably over time.

This thesis is divided into two separate manuscripts, both of which are in the format for publication in an American Fisheries Society journal. The first is entitled "Estimating Proportion Mature when Immature Fish are Unavailable for Study, with Application to American Shad in the York River, Virginia". The purpose of this manuscript is to develop an unbiased maximum likelihood method for estimating a maturation schedule for American shad based on the analysis of spawning marks. Utilizing this method, maturity schedules for 1998, 1999, and 2000, as well as the three-year combined data set are estimated. This method relies on the assumption that mature and immature survival for fish of a given age are equal. Since the population is currently under moratorium, this assumption appears to be met.

The second manuscript is entitled "Interpreting Maturation Data for American Shad in the Presence of Fishing Mortality - A Look at Historical Data from the York River, Virginia". This manuscript develops another maximum likelihood model for estimating maturation parameters during historical and recent periods of commercial fishing when mature survival does not equal immature survival for a given age. This model is illustrated by analyzing what maturity looked like in 1959 based on historical data presented in Nichols and Massmann (1963). This manuscript provides understanding of how a population might respond, in terms of maturation, to exploitation, as well as understanding the state of a stock at various times in the past. This understanding can serve as an aid in further developing restoration targets.
LITERATURE CITED


CHAPTER 2. ESTIMATING PROPORTION MATURE WHEN IMMATURE FISH ARE UNAVAILABLE FOR STUDY, WITH APPLICATION TO AMERICAN SHAD IN THE YORK RIVER, VIRGINIA
Estimating Proportion Mature at Age When Immature Fish are Unavailable for Study,

with Application to American Shad in the York River, Virginia

Kristin L. Maki, John M. Hoenig, and John E. Olney, Sr.

Virginia Institute of Marine Science, The College of William and Mary

PO Box 1346, Gloucester Point, VA 23062
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. Here we develop a model to estimate the maturation schedule for American shad 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 is used to estimate the probabilities of shad maturing at given ages. Shad collected in this study matured between the ages of three and seven. The proportions maturing at these ages are estimated for data collected during 1998 (1.8%, 26.3%, 52.4%, 19.5%, 0% maturing at 3,...7 years), 1999 (5.4%, 41.0%, 31.6%, 13.3%, 8.7%), and 2000 (0.3%, 27.3%, 49.6%, 18.0%, 4.8%), as well as for the three-year combined data set (2.1%, 32.5%, 44.5%, 16.8%, 4.1%). Maturity schedules are constructed by cumulating the maximum likelihood estimates and are found to generally overlap for the three 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 percent of immature survival.
Introduction

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 and immature fish are unavailable. Without a method of inferring what immature fish are still at sea during the spawning season, unbiased estimation of a maturity schedule is impossible.

The American shad (Alosa sapidissima) is an anadromous clupeid, spending most of its life in the sea and ascending coastal rivers to spawn. American shad on the Atlantic coast range from the St. Johns River, Florida, to the St. Lawrence River, Canada (Walburg 1960). Young-of-the-year shad emigrate from natal rivers during fall and remain in oceanic waters until they reach sexual maturity. Most sexually mature fish return to the streams of their birth 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 fresh water to spawn (Moss 1946; Cating 1953; Judy 1961). It has generally been accepted that shad eat very little while in freshwater and that growth of the shad ceases during the spawning migration. Annuli are recognized on scales of many 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 which have previously spawned. Judy (1961) validated the ageing method of Cating (1953) which uses annuli and spawning marks to determine total age of shad.

Spawning marks have been utilized in previous studies (in conjunction with annuli) to investigate age at maturity by noting the first appearance of the mark on scales of collected fish. For example, Leggett (1969, his Table 5) sampled 275 female shad in 1967 and 1968 from the York River and utilized 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. He 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
proportion mature at age because the data are incomplete wherever there is a dash in the
table. Using the example in Table 1, for the cohorts hatched from 1994 to 1997 and
collected in 2000, observations on numbers mature at some ages have yet to be made.

In theory, one could examine fish of a single age which has completely recruited
to the mature segment of the population to determine a maturity schedule. For example,
if nine-year-old fish represented all mature individuals that had spawned on at least a
single previous occasion, 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
due to 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 utilized 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 five
to ten years of sampling which, at present, is unavailable. As an alternative method, we
develop a cross-sectional model of one year’s sampling to estimate a maturity schedule.
We apply this model to three years of sampling (1998-2000) and expand the model to use
the three-year combined data set to increase sample size and estimate an "average"
maturity schedule. The method of maximum likelihood is 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, utilizing a staked gill net as part of an ongoing monitoring and stock assessment study (Olney and Hoenig, in press). The 273-m (900-ft) net was constructed of 12.4-cm (4 7/8") stretched-mesh monofilament netting. The net was fished two days per week throughout the spawning period. All shad caught in the net were brought back to the lab for examination and collection of biological data. Only the data for female shad were used for this study. Acetate impressions of shad scales were read on a microfilm projector using Cating’s (1953) method for determining age of shad and identifying spawning marks. For each fish, the age at capture and the age of first spawning were recorded. For example, a six-year-old fish captured in 1999 with two spawning checks must have spawned for the first time in 1997 at age four. It would be spawning for the third time but would not yet show evidence of a third spawning mark.

Development of the Model

We estimate the proportion of the shad population becoming mature at each age from the ages and previous spawning histories of samples collected in one year (for each year of sampling), as well as from the three-year combined data set. The method makes the assumption that fish of all year-classes follow similar maturation schedules. Thus, for example, scales from fish that were six years old in 1999 will contain the same spawning
history information (number of spawning marks) as those from fish that were age six in all other years. In all three years of sampling, mature shad younger than age three were not observed and the oldest virgin was age seven (Table 1). Thus, we assume that the proportions maturing before age three and after age seven are zero. Three other assumptions underlie the model. First, it is assumed that there is no difference in mortality between immature and mature fish of a given age. This implies there is no spawning stress-induced mortality and there is no fishing mortality during the run. It also implies that there is no by-catch (fishing) mortality of immature shad. Second, mature shad do not skip years of spawning. Finally, early maturing fish have the same catchability as late maturing fish of the same age. This implies equal size; that is, a five-year-old fish that matured at three is the same size as a five-year-old virgin.

To formally develop the model, let \( x_{ij} \) be the number of fish captured at age \( i \) (\( i = 3, ..., 10 \)) spawning for the first time at age \( j \) (\( j = 3, ..., 7 \)), and \( p_j \) be the probability of 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 ten-year-old fish is the product of the probabilities for each individual spawning history within that set. A ten-year-old fish must fall into one of five spawning history categories, the categories defined by the ages of maturity (i.e., ages 3 to 7). Thus, the observations on ten-year-olds constitute a sample from a multinomial distribution under simple random sampling of mature ten-year-olds, and the likelihood for ten-year-old fish is

\[
\Lambda_{10} \propto \prod_{j=3}^{7} p_j^{x_{10j}}.
\]
The likelihoods for ages seven, eight, and nine are constructed the same way. Hence, for \( i = 7, 8, 9, \) and 10, the likelihood is given by

\[
\Lambda_i \propto \prod_{j=3}^{7} p_j^{x_{ij}}. \tag{2}
\]

Observations on the six-year-old fish are incomplete because we see the relative proportions maturing at ages three, four, five, and six but don’t observe that portion of the year class that will mature at age seven. Consequently, the likelihood for fish of age six is

\[
\Lambda_6 \propto \left( \frac{p_6}{1 - p_7} \right)^{x_{66}} \times \left( \frac{p_5}{1 - p_7} \right)^{x_{65}} \times \left( \frac{p_4}{1 - p_7} \right)^{x_{64}} \times \left( \frac{p_3}{1 - p_7} \right)^{x_{63}} \tag{3}
\]

\[
= \prod_{j=3}^{6} \left( \frac{p_j}{1 - p_7} \right)^{x_{6j}}.
\]

Similarly, for five-year-old fish, we can’t observe the proportion maturing at age six or seven. 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 four-year-old fish we have

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

Since the age-specific probabilities of maturing must sum to one, we know
\[ \sum_{i=3}^{7} p_i = 1. \]  \hspace{1cm} (6)

Therefore, in equations 1-5 above, \( p_7 \) can be replaced by the expression

\[ p_7 = 1 - \sum_{i=3}^{6} p_i. \]  \hspace{1cm} (7)

Since the probabilities associated with the various ages of maturity are all independent, the overall likelihood, denoted by \( \Lambda \), is simply the product of the individual likelihoods. Hence we have,

\[ \Lambda = \prod_{i=4}^{10} \Lambda_i. \]  \hspace{1cm} (8)

The maximum likelihood estimates are those values of the \( p_i \) (\( i = 3, \ldots, 6 \)) that maximize the likelihood function. These can be found numerically (e.g., using the Splus function \texttt{nlminb}) or analytically (see Appendix A). 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 Splus function \texttt{vcov.nlminb} written by Venables and Ripley (1999).

In addition to estimating three individual maturity 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 three years of sampling (Table 1). Now, the likelihood for four-year-old fish becomes

\[ \Lambda_4 \propto \prod_{j=3}^{4} \left( \frac{p_j}{1 - p_7 - p_6 - p_5} \right)^{\sum_{k=1}^{3} x_{ijk}}, \]  \hspace{1cm} (9)
where $k$ is the year of sampling ($k = 1998, 1999, \text{and} 2000$). The other likelihood equations (for ages five through ten) 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, $N_j$ (i.e., row sums in Table 1). For example, the expected catch for four-year-old fish maturing at the age of four is

$$E(x_{4,4}) = \frac{P_4}{1 - P_5 - P_6 - P_7} N_4.$$  (10)

Results

American shad ranged in age from three to ten years with 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 ($p_j$) derived numerically (Table 2) were equivalent to those calculated analytically. Model residuals (observed - expected) were examined and no clear patterns were detected (Figure 1). 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 three 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 three
years. The largest differences in estimates of $p_i$ were observed for ages three and four which, in 1999, were higher than in the other two years. Comparisons of maximum likelihood estimates of proportion mature with sample proportion estimates revealed consistent differences between the two methods (Figure 4). Results of a sensitivity analysis (Appendix B) 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) yield biased maturation parameters. Utilizing sample proportions (Nichols and Massmann 1963; Leggett 1969; Carscadden and Leggett 1975b) results in shifting the maturity schedule to earlier ages since observations on numbers mature at some ages have not yet been made. In our data, the sample proportion method yields 94.4 percent maturity by age five, while the maximum likelihood method estimates only 79.1 percent maturity by age five for the three-year combined sample. Hence, utilization of an invalid method based on biased samples skews the estimate of maturity to earlier ages. The proposed maximum likelihood method yields 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 marks. This is
because the absorption process does not affect the posterior portion of the scale to the
same extent as the anterior portion. A spawning mark may erode away 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 which 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, due to
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 shad of a given age maturing
in different years. The test was based on a comparison of mean total lengths for each age
category of shad (Figure 5). Total lengths were used instead of weights due to
differences in weights within an age category that are attributable to differential stages of
gonad maturation.

The assumption that there is no difference in mortality between immature and
mature fish of a given age is somewhat problematic. Fishing for shad in the Chesapeake
Bay region has been under moratorium since 1980 in Maryland and 1994 in Virginia.
This leaves the modest, mixed-stock, offshore intercept fishery as the largest possible
source of differential fishing mortality on the York River population (Olney and Hoenig,
in press). At present, there is no direct evidence of fishing mortality on immature fish,
although some bycatch mortality might occur. Spawning stress could also cause
studied the bioenergetics of American shad homing to the St. Johns (Florida), York, and
Connecticut rivers, and found that American shad consumed 30 to 80 percent 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 Connecticut and Florida shad, suggesting that York River shad
may have energy reserves available for the postspawning migration. Because of the
proximity of spawning grounds on the York River system (Bilkovic et al., in review),
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% (390 of 876) of fish sampled here had at least one prior spawn) 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)
reported by Leggett and Carscadden (1978). However, Leggett and Carscadden’s
observations were made when an active fishery was in operation and the 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 ($R = 0.5$ to $1.0$) (see Appendix B) 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 one were not considered.

Differences between actual and estimated proportions maturing at age $j$ were largest for fractions maturing at ages four and five (Figure B-1). By the age of seven, no departures from 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 proportion mature at age $j$ (Figure B-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 $R$ equals 1.0.

Maturity estimates for 1998, 1999, and 2000 were grossly similar, with the exception that ages three and four in 1999 differed from the other two 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. Eventually, with enough years of data, the maximum likelihood method can be used in a longitudinal study, estimating maturity for one year
class throughout time. The cross-sectional approach will still retain it’s 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 utilized 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 since 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 since each age is investigated independently.

This method is an important advance in determining maturation schedules in some anadromous fishes. However, further information is required to fully develop the model. While the moratorium on in-river fishing reduces the differential survival between mature and immature shad, the level of fishing mortality offshore is unknown. Additionally, although Garman (1992) suggested that carcasses of dead clupeids are an important source of marine-derived energy in Virginia rivers, there is no direct evidence of post-spawning mortality of York River American shad. Estimates of relative survival rates for mature and immature shad are currently unavailable. If these estimates could be made, the accuracy of the maturity model would increase.
Acknowledgments

We thank Dennis Heisey (University of Wisconsin) for suggesting the analytic procedure in Appendix A, Dan Hepworth (VIMS) for his assistance in programming, Kathy Hattala (New York State Department of Environmental Conservation) for assistance in interpreting scales, Raymond and Tony Kellum for assistance in the field, members of the VIMS Anadromous Fishes Laboratory for assistance in processing samples, and David Secor (University of Maryland Center for Environmental Sciences), Peter VanVeld (VIMS) and Robert Latour (VIMS) for their helpful reviews. This research was funded by the Wallop-Breaux Program of the U.S. Fish and Wildlife Service through the Marine Recreational Fishing Advisory Board of the Virginia Marine Resources Commission (Grant Numbers F-116-R-1 and F-116-R-2), and by the Anadromous Fish Conservation Act, Public Law 89-304 (Grant-In-Aid Project AFC-28, Grant Number NA86FA0261 and Project AFC-30, Grant Number NA96FA0229) from the National Marine Fisheries Service. This manuscript is a portion of a thesis prepared by the senior author in partial fulfillment of the requirements for the degree of Master of Science, School of Marine Science, College of William and Mary. This is VIMS contribution No. ****.
Literature Cited


Glebe, B.D., and W.C. Leggett. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (Alosa sapidissima) and
their life history consequences. Canadian Journal of Fisheries and Aquatic Sciences 38:806-820.


Olney, J.E., and J.M. Hoenig. In Press. Managing a fishery under moratorium:

assessment opportunities for Virginia stocks of American shad (*Alosa sapidissima*). *Fisheries*.


Appendix A

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

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

This is a maximum likelihood estimator of

$$\frac{P_a}{\sum_{i=3}^{10} p_i}.$$  

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 10-year-old shad collected in this study (for the 3-year combined data set):

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

$e_{10}$ estimates $\hat{p}_{10}$, thus

$$\hat{p}_{10} = 0.$$  

Similarly, for nine-year-old fish,
\[ e_9 = \frac{d_9}{R_9} = \frac{0}{6} \] estimates \[ \frac{p_9}{p_3 + p_4 + \ldots + p_9} = \frac{p_9}{1 - p_{10}}. \]

Solving for \( p_9 \) we obtain

\[ \hat{p}_9 = e_9 \ast (1 - p_{10}) = e_9 \ast (1 - 0), \]

\[ \hat{p}_9 = 0. \]

Likewise, for eight-year-old fish,

\[ e_8 = \frac{d_8}{R_8} = \frac{0}{25} \] estimates \[ \frac{p_8}{p_3 + p_4 + \ldots + p_8} = \frac{p_8}{1 - p_{10} - p_9}. \]

Solving for \( p_8 \) we obtain

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

\[ \hat{p}_8 = 0. \]

For seven-year-old fish,

\[ e_7 = \frac{3}{73} = \frac{p_7}{1 - p_{10} - p_9 - p_8}. \]

Solving for \( p_7 \),

\[ \hat{p}_7 = e_7 \ast (1 - p_{10} - p_9 - p_8) = \frac{3}{73} \ast 1 = 0.0410959. \]

For six-year-old fish,

\[ e_6 = \frac{47}{268} = \frac{p_6}{1 - 0 - 0 - 0.0410959}; \hat{p}_6 = 0.168166 \]

and so on.
Appendix B

Sensitivity Analysis

Estimation of the maturity parameters in the likelihood model assumed a ratio of mature to immature survival, R, equal to one. 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 of maturing shad of age $j$ divided by the total number surviving to age $j$, i.e.,

$$
p_j = \frac{\text{# maturing}}{\text{# maturing} + \text{# already mature} + \text{# remaining immature}}.
$$

Thus, when $R=1$, if 90% of the shad at age four are mature then no more than 10% of the shad at age five 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 one. For example if 90% of shad at four are mature but survival of mature four-year-olds after the spawning run is zero ($R = 0$), the proportion maturing at five, $p_5$, can be as high as 100%. We can define conditional maturation rates, $\pi_j$, to be the probability a fish of age $j$ matures during the year given that it is immature, i.e.,

$$
\pi_j = \frac{\text{# age } j \text{ maturing}}{\text{# age } j \text{ maturing} + \text{# age } j \text{ remaining immature}}.
$$
These conditional rates do not vary with the survival ratio, $R$, 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 ($R = 0.5, ..., 1.0$) was used to test how the parameters 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 $R=1$ were set equal to \{0.021, 0.325, 0.445, 0.168, 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 \texttt{nlminb} in Splus).

Let $X$ be the number of three-year-old 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 $j$ ($i = 3, ..., 10; j = 3, ..., i$), $N_i$ 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, $\rho_j^{(r)}$ be the true fraction maturing at age $j$ when $R=r$, $\hat{\rho}_j^{(r)}$ be the estimated proportion maturing at age $j$ when $R$ is assumed to be 1 but is really $r$, $m_j^{(r)}$ be 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 $r = 1$. Since all shad are immature at 2, the unconditional and conditional probabilities of maturing at three are the same, and

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

$\pi_4$ is the probability that a shad matures at age four given that it is immature when it turns four years old. Thus,

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

Similarly for shad maturing at age five and six,

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

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

For York River shad, all fish matured by 7. Thus,

$$\pi_7 = 1.$$

Since the conditional maturation rates are independent of the level of exploitation, thus remaining 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 four-year-old fish from the spawning run contained shad maturing at the age of three and at the age of four. Those maturing at three have undergone one
year of mature survival since age three, while those maturing at four have undergone one year of immature survival. Thus, the expected catch of four-year-olds maturing at three is

\[
E(x_{4,3}) = N_4 \frac{X \pi_3 S_M}{X \pi_3 S_M + X \pi_4 (1 - \pi_3) S_I} = N_4 \left( \frac{\pi_3 R}{\pi_3 R + \pi_4 (1 - \pi_3)} \right)
\]

and the expected catch of four-year-olds maturing at four is

\[
E(x_{4,4}) = N_4 \frac{X \pi_4 (1 - \pi_3) S_I}{X \pi_3 S_M + X \pi_4 (1 - \pi_3) S_I} = N_4 \left( \frac{\pi_4 (1 - \pi_3)}{\pi_3 R + \pi_4 (1 - \pi_3)} \right).
\]

The expected catches for five-year-olds for a fixed value of \( R \) become

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

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

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

This process was carried out similarly to fill in the rows of the new tables for age of capture equal to six, seven, eight, nine and ten. Maximum likelihood estimates \( \hat{p}_j^{(a)} \) were computed under the assumption that \( R=1 \) when the true values of \( R \) ranged from 0.5 to 1.0 by utilizing the Splus function nlminb (Figure B-1). These biased estimates can be compared to the true fraction maturing at age \( p_j^{(a)} \) which are based on the \( \pi_j \) values and the level of \( R \). The true fraction maturing at age are computed as follows
Thus, \[ p_j^{(r)} = \frac{\# \text{ maturing at age } j}{\# \text{ matured at 3 & survived} + \# \text{ maturing at 4} + \# \text{ remain immature}}. \]

Thus, \[ p_3^{(r)} = \pi_3, \]
\[ p_4^{(r)} = \frac{\pi_4(1-\pi_3)}{\pi_3 R + \pi_4(1-\pi_3) + (1-\pi_3)(1-\pi_4)}, \]
\[ p_5^{(r)} = \frac{\pi_5(1-\pi_3)(1-\pi_4)}{\pi_3 R + \pi_4(1-\pi_3)R + \pi_5(1-\pi_3)(1-\pi_4) + (1-\pi_3)(1-\pi_4)(1-\pi_5)}, \]

and so on for the true proportions maturing at ages six and seven. When \( R \) is wrongfully assumed to be equal to one, the estimates of proportion maturing depart from the true fraction maturing at age \( j \) (Figure B-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 seven.

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

\[ m_4^{(r)} = \frac{\pi_3 R + \pi_4(1-\pi_3)}{\pi_3 R + \pi_4(1-\pi_3) + (1-\pi_3)(1-\pi_4)}, \]
\[ m_5^{(r)} = \frac{\pi_3 R^2 + \pi_4 (1 - \pi_3) R + \pi_5 (1 - \pi_3)(1 - \pi_4)}{\pi_3 R^2 + \pi_4 (1 - \pi_3) R + \pi_5 (1 - \pi_3)(1 - \pi_4) + (1 - \pi_3)(1 - \pi_4)(1 - \pi_5)}, \]

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

\[ m_7^{(r)} = 1. \]

Again, the greatest differences between actual and estimated values of proportion mature occurred for ages four and five, while the differences were minimal for age six, and zero for age seven (Figure B-2). Additionally, large values of R (>0.75) resulted in little distinction between the true and estimated values.

Values of \( \beta_j^{(r)} \) 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. Underestimates of \( \pi_j \) (which are considered independent of the magnitude of R) are obtained when it is not recognized that R ≠ 1 (Figure B-3).
Figure B-1. Comparison of true fraction maturing at age (broken line) with estimated fraction maturing at age (solid line) for levels of $R$ between 0.5 and 1.0.
Figure B-2. Comparison of actual proportion mature by age (broken line) with estimated proportion mature by age (solid line) for levels of R between 0.5 and 0.95. At R = 1, the two curves are equal.
Figure B-3. Estimates of $\pi_j$ calculated from the biased estimations of fraction mature at age (achieved by wrongfully assuming $R = 1$). True $\pi_j$ is value where $R = 1.0$. 
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 combined data set.

Table entries are numbers of fish. Ages are based on scale analysis.

<table>
<thead>
<tr>
<th>Age at Capture</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998 3</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>73</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>40</td>
<td>83</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>10</td>
<td>27</td>
<td>14</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>8</td>
<td>9</td>
<td>1</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Age at Capture</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>1999 3</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>18</td>
<td>32</td>
<td>10</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>72</td>
<td>51</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>33</td>
<td>26</td>
<td>14</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>7</td>
<td>5</td>
<td>0</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Age at Capture</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>2000 3</td>
<td>9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>107</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>30</td>
<td>100</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>36</td>
<td>18</td>
<td>16</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>3</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age at Capture</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Combined 3</td>
<td>12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>193</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>142</td>
<td>234</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>79</td>
<td>71</td>
<td>44</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>18</td>
<td>25</td>
<td>2</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>8</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>0.018</td>
<td>0.006</td>
<td>0.054</td>
<td>0.013</td>
<td>0.003</td>
<td>0.002</td>
<td>0.021</td>
<td>0.004</td>
</tr>
<tr>
<td>4</td>
<td>0.263</td>
<td>0.030</td>
<td>0.410</td>
<td>0.041</td>
<td>0.273</td>
<td>0.032</td>
<td>0.325</td>
<td>0.020</td>
</tr>
<tr>
<td>5</td>
<td>0.524</td>
<td>0.040</td>
<td>0.316</td>
<td>0.036</td>
<td>0.496</td>
<td>0.043</td>
<td>0.445</td>
<td>0.023</td>
</tr>
<tr>
<td>6</td>
<td>0.195</td>
<td>0.044</td>
<td>0.133</td>
<td>0.034</td>
<td>0.180</td>
<td>0.040</td>
<td>0.168</td>
<td>0.023</td>
</tr>
<tr>
<td>7</td>
<td>0.000</td>
<td>0.000</td>
<td>0.087</td>
<td>0.059</td>
<td>0.048</td>
<td>0.046</td>
<td>0.041</td>
<td>0.023</td>
</tr>
</tbody>
</table>
Figure 1. Residuals from the maximum likelihood estimation of proportions maturing based on the three-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 three-year combined data set.
Figure 3. Proportion of American shad mature by a given age as represented by 95% confidence intervals (± 2 standard errors) for 1998 (triangles), 1999 (circles), and 2000 (squares).
Figure 4. Comparison of estimates of proportion mature at age by the maximum likelihood method (broken lines) and by taking sample proportions (solid lines) for 1998, 1999, 2000, and the combined three-year data set.
Figure 5. Mean total length in mm per age/spawning category of American shad collected in the York River, Virginia, during 1998, 1999, and 2000. Age/spawning category a.b represents fish of age a that have spawned b times prior to capture. Numbers above bars refer to number of fish examined. Examination of age category and lengths in individual years yielded similar patterns to the combined data (see Maki 2000).
CHAPTER 3. INTERPRETING MATURATION DATA FOR AMERICAN SHAD IN THE PRESENCE OF FISHING MORTALITY - A LOOK AT HISTORICAL DATA FROM THE YORK RIVER, VIRGINIA
Interpreting Maturation Data for American Shad in the Presence of Fishing Mortality -
A Look at Historical Data from the York River, Virginia

Kristin L. Maki, John M. Hoenig, and John E. Olney, Sr.
Virginia Institute of Marine Science, The College of William and Mary
PO Box 1346, Gloucester Point, VA 23062
Abstract

To enable better monitoring, forecasting, and the setting of restoration targets, we began a study of maturation by American shad (*Alosa sapidissima*) in the York River, Virginia. Throughout the course of the study, the need for historical information about the status of the stock, and how it relates to the current declined state, became evident. We identified an early study (Nichols and Massmann 1963) that might allow reconstruction of maturation schedules for historical time periods and enable comparison with contemporary maturation schedules. During a commercial fishery, mature survival can differ from immature survival for a given age. 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 and this 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 Nichols and Massmann). The estimated maturation parameters for 1959 were higher than at present. We concluded that either shad matured earlier in 1959 or that the estimated exploitation rate given by Nichols and Massmann was too high.

Introduction

The scales of American shad (*Alosa sapidissima*) and other alosine fishes that have previously spawned exhibit spawning marks. These marks are characteristic scarlike rings on the scale and are presumed to be caused by erosion or absorption of the scale when the shad enters fresh water to spawn. The presence of spawning marks has been used to determine the age of a fish, at what age 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. Specifically, 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 sex and age composition, as well as repeat spawning information (for states north of South Carolina) (ASMFC 1999). However, the implications 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 other years when a strong year class matures and joins the spawning migration. Second, if exploitation rate was high in the previous year, then the number of repeat spawners in the current year will be low. Third, for American shad, southern stocks are largely semelparous. Shad native to rivers at latitudes north of 32°N exhibit increasing levels of iteroparity with increasing
latitude of the natal river (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 age of maturation for the American shad (see, for example, Nichols and Massmann 1963; Leggett 1969). Estimates of percent 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. (in review) showed that such data alone provide biased estimates of the percentages maturing at each age. However, they were able to develop a model utilizing the method of maximum likelihood to estimate the maturation schedule from data on age at capture and age at first spawning. In order to obtain unbiased maturation estimates from samples taken from the spawning run, however, one must be able to assume that the mortality rates for mature and immature fish of the same age are equal. This assumption appeared reasonable for the case studied by Maki et al. (in review) because the stock they studied was under a moratorium for in-river harvesting of shad. Because of the moratorium, in-river fishing mortality on mature fish is largely absent and mature fish are subject only to offshore intercept fisheries. Thus, the moratorium helps assure that the assumption of equal mortality rates is met by eliminating one source of differential mortality (Olney and Hoenig, in press). Differential mortality between immature and mature fish could also arise due to the unknown stress associated with spawning. However, York River American shad undergo a relatively short migration to the spawning grounds (Bilkovic et al., in review), spawn repeatedly (Maki et al., in review), may have energy reserves
available for the postspawning migration (Glebe and Leggett 1981), and therefore do not appear to have high spawning induced mortality.

Our study of shad spawning marks was motivated by the need to develop monitoring, forecasting and restoration plans for American shad in Virginia’s rivers. Our first step was to develop a maturation schedule for shad (Maki et al., in review). This information is useful for forecasting in two ways. When an especially strong or weak year class appears in juvenile monitoring, we would like to know when the effects will be felt in the spawning runs. Also, to forecast next year’s run size from the current year’s run data, we need to know how the maturation of each cohort will proceed.

Therefore, it is useful to know if maturation rates change appreciably over time. We are attempting to review all historic information about the status of the Virginia stocks in an attempt to piece together a history of maturation schedules. This paper describes our attempts to interpret historical information collected by Nichols and Massmann (1963) on maturation by the American shad in the York River, Virginia. These data were collected during a time of heavy commercial fishing and thus require a maturity model that accounts for a value of the ratio of mature to immature survival not equal to one. The development of such a model will not only enhance interpretation of historical maturation data, but will allow interpretation of current maturation data for populations where commercial fishing occurs (and hence, the survival of mature fish does not equal the survival 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 use in the maximum likelihood model to estimate a historical maturity schedule. 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 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 non-negative integers, there is a finite number of solutions that yield the required column sums, row sums, 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 program).

All attempts at reconstructing a data matrix for the three years of data presented in Nichols and Massmann failed. It was impossible to assign non-negative 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 by Nichols and Massmann during 1959 was obtained from the National Marine Fisheries Service in
Beaufort, NC. Data summaries were recalculated from the raw data and were used to determine where Nichols and Massmann had made errors (Table 2).

Based on notes contained in the microfilm, it was possible to hypothesize how Nichols and Massmann had created errors in the data summaries. The total numbers of females captured at age were apparently tallied quite carefully. This is reflected by the fact that no differences were found for this total as calculated by Nichols and Massmann and our recalculations (Table 2). The tallies for number of spawning marks (for males and females) 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 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 data, the recalculated summaries were utilized in the estimation of maturity 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.

**Development of the Maturity Model**

Maki et al. (in review) devised a maximum likelihood model that estimates proportion maturing at age j ($\hat{p}_j$) when the value of the ratio (R) of mature to immature
survival equals one. During times of commercial fishing, it is extremely likely that this ratio will depart from a value of one. Estimating 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 rate between mature and immature fish. For example, if 90% of shad at four are mature but survival of mature four-year-olds after the spawning run is zero (R=0), the proportion maturing at five can be as high as 100% and the $p_j$ no longer sum to one.

Thus, in order to examine maturity during historical periods of commercial fishing, when $R \neq 1$, a different characterization of maturation is convenient. Therefore, we define conditional maturation rates, $\pi_j$, to be the probability a fish of age $j$ matures during the year given that it is immature, i.e., (for $j = 1, ..., i$),

$$
\pi_j = \frac{\# \text{ age } j \text{ maturing}}{\# \text{ age } j \text{ maturing} + \# \text{ age } j \text{ remaining immature}}.
$$

These conditional rates do not vary with the survival ratio, $R$, except inasmuch as the basic biology might change. We estimate the conditional maturation rates for the data collected by Nichols and Massmann with a maximum likelihood model.

To formally develop the model, let $x_{ij}$ be the number of fish captured at age $i$ ($i = 3, ..., 7$) spawning for the first time at age $j$ ($j = 3, ..., i$), and $\pi_j$ be the conditional probability of maturation at age $j$ given a fish is age $j$ and immature. 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 four-year-old fish is

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

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

The first factor gives the proportion of fish that matured at age three. This is equal to the
number of fish that matured at age three and survived divided by the sum of the number
that matured at three and survived plus the number that remained immature at age three,
survived to age four and are maturing at age four. 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 four
divided by the sum of the number maturing plus the number already mature. The
likelihood $\Lambda_4$ is a binomial. Thus, the second term can be expressed as one minus the
first term. A constraint such as this is necessary to obtain the maximum likelihood
estimates.

Thus, the likelihood for five-year-old fish is

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

where
\[ A = R^2 \pi_3 \]
\[ B = \pi_4 (1 - \pi_3) R \]
\[ C = \pi_5 (1 - \pi_3)(1 - \pi_4). \]

The three factors represent the probabilities of maturing at three, four, and five, respectively, given that a fish is age five and mature. Similar expressions hold for ages six and seven. The overall likelihood, denoted by \( \Lambda \) 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., in review) to female shad samples collected in 1998, 1999, and 2000 in the York River, Virginia, during the spring spawning run (Table 1). Estimates of proportion mature (\( p_j \)) were derived numerically, utilizing the S-plus nlminb function (Table 3). These values were computed under the presumably correct assumption that \( R=1 \) (since the population is currently under a moratorium for in-river fishing) and were utilized to calculate values of \( \pi_j \) for the combined 1998-2000 data (see Appendix B in Maki et al. 2000, in review) (Table 3).

Since reconstruction of data matrices for most of the annual data collected by Nichols and Massmann (1963) was impossible due to errors in the published data, estimation of \( \pi_j \), utilizing the maximum likelihood model described above was completed only for the female data collected in 1959. Nichols and Massmann estimated an
exploitation rate of about 55% for 1959. Exploitation rate is related to the ratio of mature
to immature survival and can be utilized to estimate R.

Let $\mu$ be exploitation rate, $M$ be instantaneous natural mortality (per year), $F$ be
instantaneous fishing mortality (per year), $S$ be annual survival, and let $m$ index mature
survival, and $i$ index immature survival. The shad fishery can be interpreted as a type one
fishery (Ricker 1975) where 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

$$\mu = 1 - e^{-F}.$$  \hspace{1em} (1)

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

$$S_i = e^{-M}.$$  \hspace{1em} (2)

Mature shad experience both fishing and natural mortality. Hence,

$$S_m = e^{-M-F}.$$  \hspace{1em} (3)

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

$$R = e^{-F} = 1 - \mu.$$  \hspace{1em} (4)

Thus, Nichols and Massmann’s estimate of $\mu = 0.55$ yields a value of $R = 0.45$.

Various values of $R$ were utilized in the estimation of $\pi_j$ for Nichols and
Massmann’s 1959 data, including the value of 0.45 which is predicted by their estimate
of exploitation rate. These were then compared to the values of $\pi_j$ computed from the
current maturation regime (1998-2000) (Table 3).
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. Reconstruction of the entire data table is not required in order to use the maximum likelihood procedure described in Maki et al. (in review, see Appendix A) for estimating proportions mature. However, had we chosen to use only the minimal 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 \( \pi_j \) for Nichols and Massmann’s 1959 data were made utilizing various levels of \( R \). The values of \( \pi_j \) 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 \( \pi_j \) are not greatly altered. The estimates of \( \pi_6 \) were difficult to determine precisely. Changes in the initial guesses utilized by the maximizing Splus function could result in small changes in the value of \( \pi_6 \). This may be due in part to the small sample size of six-year-olds collected by Nichols and Massmann.

Analysis of Nichols and Massmann’s estimate of an exploitation rate for 1959 yielded an \( R \) value of 0.45. The \( \pi_j \) estimated utilizing this value of \( R \) were higher than those derived from recent years. If the biological maturity of American shad in the York River has not changed and \( R \) really equaled 0.45, then Nichols and Massmann ought to
have collected data that produced resulting $\pi_j$ estimates that resembled the current estimates. But, because their results are not similar, it suggests that either 1) $R$ was much higher than 0.45 (and the exploitation rate much lower than 0.55) during 1959 or 2) maturity has changed since 1959.

It is not clear how Nichols and Massmann could have overestimated the exploitation rate. The exploitation rate was estimated from results of a tagging and recovery study completed in 1959. 842 shad were tagged and a total of 334 shad were recaptured in the York system, while 118 shad were recaptured from areas outside the York River system. Based on an estimated outside fishing rate of 50 percent, Nichols and Massmann assumed that 236 shad tagged at the mouth of the York River were en route to other river systems. Thus, they subtracted this number from the number tagged (along with one other fish which was determined not to have spawned in the York). Nichols and Massmann divided 334 by 650 (the number of tagged fish assumed to enter the York River for the purpose of spawning) to obtain the estimation of exploitation rate. If Nichols and Massmann had instead assumed that 724 (842-118 recaptures outside of the York) shad had entered the river and 334 fish were recaptured in the river, an exploitation rate of 46 percent would have been estimated. This estimate, while yielding estimates of $\pi_j$ closer to the current estimates of $\pi_j$, is still different from the current estimate.

On the other hand, differences in maturation schedules are also difficult to explain. The results of this study suggest that, if Nichols and Massmann’s estimate of exploitation rate is correct, shad matured earlier in 1959 than in current times. It is not
unlikely that maturation of shad could have occurred at early ages during periods of strong commercial fishing. By reducing stock biomass, exploitation could release a fish stock from some pressures of intraspecific competition. This could enable faster growth and earlier maturation if maturation is size dependent (Law 2000). What is unexpected, however, is that maturation of American shad in the York system could have been "restored" to later ages since the moratorium on fishing in the York system has only been in effect since 1994. This seems a rather short time period for such changes in maturation to take place.

Neither possibility (earlier maturation or an erroneous estimate of \( \mu \)) can be absolutely supported or refuted by the results of this study. It is possible that, if historical data from the period around 1959 could be obtained from other systems, comparative analyses could be made with the estimates found in this study. It may well be that the results from other systems could also indicate maturation at earlier ages. At present, however, this information is unavailable.

The model developed here is not only useful for interpreting historical maturation data but could 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 an estimate of the ratio of mature to immature survival of shad of a similar age can be made, then the maturity model introduced here can be used to estimate \( \pi_j \). 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, a well designed and
implemented in-river tagging study could provide an estimate of exploitation rate, and subsequently an estimate of R. This value of R, and observations on mature samples collected during the spawning run, can then be utilized in the maximum likelihood estimation of \( \pi_j \). Thus, the model allows comparisons of maturation parameters at any point in history and for any rate of exploitation, provided that R is estimable.

**Acknowledgments**

We thank Patti Marraro and Joseph Smith (NOAA, Beaufort Laboratory) for assistance in procuring the original versions of the historical data and Alex Hoenig for developing the C++ code used to reconstruct data tables. This research was funded by the Wallop-Breaux Program of the U.S. Fish and Wildlife Service through the Marine Recreational Fishing Advisory Board of the Virginia Marine Resources Commission (Grant Numbers F-116-R-1 and F-116-R-2), and by the Anadromous Fish Conservation Act, Public Law 89-304 (Grant-In-Aid Project AFC-28, Grant Number NA86FA0261 and Project AFC-30, Grant Number NA96FA0229) from the National Marine Fisheries Service. This manuscript is a portion of a thesis prepared by the senior author in partial fulfillment of the requirements for the degree of Master of Science, School of Marine Science, College of William and Mary. This is VIMS contribution No. ****.


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. (Summarized from Maki et al in review.)

<table>
<thead>
<tr>
<th>Age at Capture</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>193</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>142</td>
<td>234</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>79</td>
<td>71</td>
<td>44</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>18</td>
<td>25</td>
<td>2</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>8</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 2. Catch and spawning data collected from York River American shad samples.

1959 P (published) data are adapted from Table 7 in Nichols and Massmann (1963);
1959 R (revised) data are adapted from a microfilm reel containing the raw data collected by Nichols and Massmann. Entries in table are numbers of fish.

<table>
<thead>
<tr>
<th></th>
<th>1959 P Males</th>
<th>1959 P Females</th>
<th>1959 R Males</th>
<th>1959 R Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total age at capture:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 years</td>
<td>35</td>
<td>19</td>
<td>35</td>
<td>19</td>
</tr>
<tr>
<td>4</td>
<td>190</td>
<td>398</td>
<td>191</td>
<td>398</td>
</tr>
<tr>
<td>5</td>
<td>99</td>
<td>154</td>
<td>98</td>
<td>154</td>
</tr>
<tr>
<td>6</td>
<td>21</td>
<td>25</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>8</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>350</td>
<td>599</td>
<td>349</td>
<td>599</td>
</tr>
<tr>
<td>Age at first spawning:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 years</td>
<td>128</td>
<td>32</td>
<td>133</td>
<td>32</td>
</tr>
<tr>
<td>4</td>
<td>211</td>
<td>447</td>
<td>208</td>
<td>439</td>
</tr>
<tr>
<td>5</td>
<td>11</td>
<td>112</td>
<td>8</td>
<td>121</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>350</td>
<td>599</td>
<td>349</td>
<td>599</td>
</tr>
<tr>
<td>Number of times previously spawned</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>193</td>
<td>526</td>
<td>192</td>
<td>525</td>
</tr>
<tr>
<td>1</td>
<td>83</td>
<td>58</td>
<td>82</td>
<td>57</td>
</tr>
<tr>
<td>2</td>
<td>65</td>
<td>15</td>
<td>67</td>
<td>17</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>350</td>
<td>599</td>
<td>349</td>
<td>599</td>
</tr>
</tbody>
</table>
Table 3. Estimates of conditional maturation at age parameters derived from 1959 data collected by Nichols and Massmann and from current data. Dashes indicate Nichols and Massmann did not collect any fish maturing at the age of seven; all seven-year-old fish in the current study were mature so the conditional maturation probability is assumed to be 1.0.

<table>
<thead>
<tr>
<th>π</th>
<th>R=1</th>
<th>R=0.9</th>
<th>R=0.8</th>
<th>R=0.7</th>
<th>R=0.6</th>
<th>R=0.5</th>
<th>R=0.45</th>
<th>R=0.4</th>
<th>R=1</th>
</tr>
</thead>
<tbody>
<tr>
<td>π₃</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.02</td>
<td>0.02</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>π₄</td>
<td>0.28</td>
<td>0.30</td>
<td>0.33</td>
<td>0.36</td>
<td>0.40</td>
<td>0.45</td>
<td>0.48</td>
<td>0.51</td>
<td>0.33</td>
</tr>
<tr>
<td>π₅</td>
<td>0.89</td>
<td>0.90</td>
<td>0.91</td>
<td>0.92</td>
<td>0.93</td>
<td>0.93</td>
<td>0.95</td>
<td>0.95</td>
<td>0.68</td>
</tr>
<tr>
<td>π₆</td>
<td>0.99</td>
<td>1.00</td>
<td>1.00</td>
<td>1.01</td>
<td>1.01</td>
<td>0.82</td>
<td>1.00</td>
<td>0.88</td>
<td>0.80</td>
</tr>
<tr>
<td>π₇</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.00</td>
</tr>
</tbody>
</table>


Glebe, B.D., and W.C. Leggett. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (Alosa sapidissima) and
their life history consequences. Canadian Journal of Fisheries and Aquatic Sciences 38:806-820.


Maki, K.L., J.M. Hoenig, and J.E. Olney. In Review. Estimating proportion mature at age when immature fish are unavailable for study, with application to American


Appendix A

Residuals from the Maximum Likelihood Estimation of Proportions of Shad Maturing

Residuals (observed-expected) from the maximum likelihood maturity model presented in Chapter 2 were examined and no clear patterns were detected (Figures A-1, A-2, and A-3). Observed and expected values are as described in Chapter 2.
Figure A-1. Residuals from the maximum likelihood estimation of proportions maturing based on the 1998 data.
Figure A-2. Residuals from the maximum likelihood estimation of proportions maturing based on the 1999 data.
Figure A-3. Residuals from the maximum likelihood estimation of proportions maturing based on the 2000 data.
Appendix B

Analysis of Equal Catchability Between Early and Late Maturing Shad of a Given Age

An assumption of the maximum likelihood model for estimating proportion mature is that early maturing fish have the same catchability as late maturing fish of the same age. This implies equal size; that is, a five-year-old fish that matured at three is the same size as a five-year-old virgin. To test for equal catchability, comparisons of mean total lengths for each age category of shad were made (Figure A-1). The visual test revealed no significant differences in size of shad of a given age maturing in different years. Total lengths were used instead of weights due to differences in weights within an age category that are attributable to differential stages of gonad maturation.
Figure B-1. Mean total length in mm per age category of American shad collected in the York River, Virginia, during 1998, 1999, and 2000. Age category a.b represents fish of age a that have spawned b times prior to capture. Numbers above bars refer to number of fish examined.
Appendix C

C++ Code for Reconstruction of Data Tables When Column, Row, and Diagonal Sums are Known

Nichols and Massmann (1963) provided summaries of the data on age at capture, age at maturity, and number of previous spawns for male and female American shad collected from the York River. It was desired, however, to have not only the summaries, but the numbers of fish captured at age i and maturing at age j, i.e., the cells of a table which result in the given spawning summaries. It is possible to construct tables similar to the one in Table 1 (Chapter 2) 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 non-negative integers, there is a finite number of solutions that yield the required column sums, row sums, and diagonal sums. The C++ program that was developed by Alex Hoenig and utilized to attempt reconstruction of the historical data obtained from Nichols and Massmann is presented here.

Three C++ source files were used in the reconstruction of a data table. The first is a header file (TABLE.H) which defines all of the functions:

/* TABLE.H
 */
 
/* Table reconstructor
 */

/* Constructs all possible bottom-triangle square tables given
 a table summary (sum of rows, cols, and diagonals).
 */
// These numbers set the maximum size of the table

#ifndef __TABLE_H__  
#define __TABLE_H__

// Adjust these to reflect the maximum size of the table
#define MAX_ROW 10
#define MAX_COL 10

#include <iostream.h>

class TableClass
{
  public:
    // constructor for this class
    TableClass (int numrows, int numcols);

    // Data access functions
    int GetNumRows () ;
    int GetNumCols () ;
    int GetNumCols () ;
    int GetData (int row, int col) ;
    void SetData (int row, int col, int val) ;
    int GetRowSum (int row) ;
    int GetColSum (int col) ;
    int GetDgnSum (int dgn) ;
    void SetRowSum (int row, int val) ;
    void SetColSum (int col, int val) ;
    void SetDgnSum (int dgn, int val) ;

    // determines whether the table fits the summaries
    bool IsValidTable () ;

    // find all solutions, check and print them
    void FindSolutions (ostream &file, bool screen) ;

    // print the table to screen or a file
    void Print (ostream &target) ;

    // print the table summary to screen or file
    void PrintSummary (ostream &target) ;

  private:
    // finds the sum of all columns before this one in this row
    int SumSoFar (int row, int col) ;
The second file (MAIN.CPP) contains the entry-point for the program, the main() function, which is where execution starts (in all console/dos-based C++ programs). This function first opens the file to be written to, prints some messages to the screen, and then inputs all the information provided by the user.
char *Message = "Table reconstructor\n----------------------\nConstructs all possible bottom-triangle tables given a table summary
(sum of rows, cols, and diagonals).\nBy Alex Hoenig, 10-22-00\nThis code is public domain.\n\n"

cout << Message;
file << Message;

int numrows=0;
// this value is the no. of rows in the table
while (numrows ==0 || numrows >= MAX_ROW) // keep asking for the size until a valid size is given
{
    cout << "Enter Y dimension of table (# of rows, maximum = " << MAX_ROW << ":");
    cin >> numrows;
    if (numrows == 0 || numrows >= MAX_ROW) // give an error message if the user entered an invalid size
        cout << "Error.\n";
}

int numcols=0;
// this value is the no. of cols in the table
while (numcols ==0 || numcols >= MAX_COL) // keep asking for the size until a valid size is given
{
    cout << "Enter X dimension of table (# of cols, maximum = " << MAX_COL << ":");
    cin >> numcols;
    if (numcols == 0 || numcols >= MAX_COL) // give an error message if the user entered an invalid size
        cout << "Error.\n";
}

TableClass Table (numrows, numcols); // holds all the table info

int x;
// this is used as a counter for some loops

int val;
// var to hold the row sums
for (x=0; x<=Table.GetNumRows()-1; x++) // loop through each row...
{
    cout << "Enter sum of row " << (x+1) << ":";
    cin >> val;
    // ...and input the sum
    Table.SetRowSum (x, val);
}
The third file (TABLE.CPP) contains a "class" called TableClass. A class represents an "object", which is a collection of data and functions. In the main function an object of type "TableClass" is created and termed "Table". Then known information about the table is retrieved from user input and entered into the table using the functions such as Table.SetRowSum (which are defined in TABLE.H). The function "FindSolutions" is
then called which in turn calls the recursive algorithm called FindRecurse. This function
is called repeatedly until all possible tables fitting the summaries are found. Valid tables
are then printed out.

/* TABLE.CPP
 * Table reconstructor
 * ---------------
 * Constructs all possible bottom-triangle square tables given
 * a table summary (sum of rows, cols, and diagonals).
 * By Alex Hoenig, 10-22-00
 * This code is public domain.
 */

#include "table.h"
#include <iostream.h>

// constructor: make a new table with the specified
// size and fill the array as much as
// necessary with 0's
TableClass::TableClass (int numrows, int numcols)
{
    NumRows = numrows;
    NumCols = numcols;
    NumSols = 0;
    for (int rp=0; rp< numrows; rp++)
        for (int cp=0; cp< numcols; cp++)
            Data [rp][cp] = 0;
}

// data access: these functions set or retrieve private data
int TableClass::GetNumRows ()
{
    return NumRows;
}

int TableClass::GetNumCols ()
{
    return NumCols;
}

int TableClass::GetNumSols ()
{
    return NumSols;
}

int TableClass::GetData (int row, int col)
{
    return Data [row][col];
void TableClass::SetData (int row, int col, int val)
{
    Data [row][col] = val;
}

int TableClass::GetRowSum (int row)
{
    return RowSums [row];
}

int TableClass::GetColSum (int col)
{
    return ColSums [col];
}

int TableClass::GetDgnSum (int dgn)
{
    return DgnSums [dgn];
}

void TableClass::SetRowSum (int row, int val)
{
    RowSums[row] = val;
}

void TableClass::SetColSum (int col, int val)
{
    ColSums[col] = val;
}

void TableClass::SetDgnSum (int dgn, int val)
{
    DgnSums[dgn] = val;
}

// check if the table matches the summary
bool TableClass::IsValidTable ()
{
    // create 3 arrays the maximum height/width/diagonals of the table
    int thisrowsum[MAX_ROW];
    int thiscolsum[MAX_COL];
    int thisdgnsum[MAX_ROW];

    // then initialize them as far as needed with 0's
    int x;
    for (x=0; x<NumRows; x++)
    {
        thisrowsum[x] = 0;
        thisdgnsum[x] = 0;
    }
for (x=0; x<NumCols; x++)
    thiscolsum[x] = 0;

// now calculate the row/col sums
for (int row=0; row < NumRows; row++)
    for (int col=0; col < NumCols; col++)
        {
            thisrowsum[row] += Data[row][col];
            thiscolsum[col] += Data[row][col];
        }

// and diagonal sums.
// first calculate the length
// and store it into vectors
int dgnlength[MAX_ROW];
for (x=0; x < NumRows; x++)
    dgnlength[x] = min (NumRows-x, NumCols);

// then iterate diagonally through the table for
// dgnlength cells, starting at each (row,0)
for (int dgn=0; dgn < NumRows; dgn++)
    {
        for (x=0; x<dgnlength[dgn]; x++)
            thisdgnsum[dgn] += Data [dgn+x] [x];
    }

// check if table conforms to the row/col/dgn summaries
for (x=0; x<NumRows; x++)
    {
        if (thisrowsum[x] != RowSums[x] || thisdgnsum[x] != DgnSums[x])
            return false;
        else
            {
                for (int y=0; y<NumCols; y++)
                    {
                        if (thiscolsum[y] != ColSums[y])
                            return false;
                    }
            }
    }

// if here, then passed all the checks, so it's found a valid table
return true;

// just output the row/col/diag. sums
void TableClass::PrintSummary (ostream &target)
{
    int x;
```cpp
// print this solution
void TableClass::Print (ostream &target)
{
    for (int x=0; x<NumRows; x++)
    {
        for (int y=0; y<NumCols; y++)
            target << Data[x][y] << "\t";
        target << endl;
    }
    target << endl;
}

// frontend for FindRecurse
void TableClass::FindSolutions (ostream &file, bool screen)
{
    Data[0][0] = RowSums[0];
    FindRecurse (file, screen, 1, 0);
}

// create all possible solutions - NOTE: almost no optimizations done here
void TableClass::FindRecurse (ostream &file, bool screen, int row, int col)
{
    if (row < NumCols-1)
    {
        if (col < row)
        {
            for (Data[row][col]=0; Data[row][col]<=RowSums[row]-
                SumSoFar(row,col); Data[row][col]++)
                FindRecurse (file, screen, row, col+1);
        }
        else // col=row
        {
            Data[row][col] = RowSums[row]-SumSoFar (row, col);
            FindRecurse (file, screen, row+1, 0);
        }
    }
    else // col=row
    { }
if (col < NumCols-1)
{
    for (Data[row][col]=0; Data[row][col]<=RowSums[row]-SumSoFar(row,col); Data[row][col]++)
        FindRecurse (file, screen, row, col+1);
} else {
    if (row < NumRows-1) {
        Data[row][col] = RowSums[row]-SumSoFar (row, col);
        FindRecurse (file, screen, row+1, 0);
    } else {
        Data[row][col] = RowSums[row]-SumSoFar (row, col);
        if (IsValidTable()) {
            NumSols++;
            Print (file);
            if (screen) Print (cout);
        }
    }
} }

// find sum of all cols before this one in the same row
int TableClass::SumSoFar (int row, int col) {
    if (col == 0) return 0;
    else return (SumSoFarRecurse (row, col-1));
}

int TableClass::SumSoFarRecurse (int row, int col) {
    if (col == 0) return Data[row][col];
    else return (Data[row][col] + SumSoFarRecurse (row, col-1));
VITA

Kristin Lynn Maki