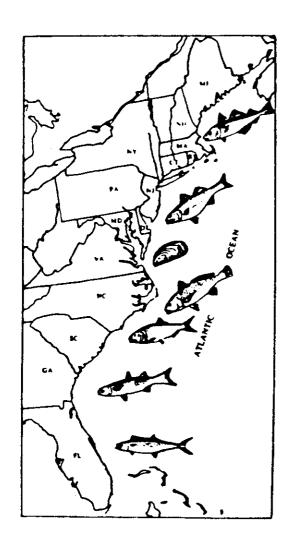
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STOCK ASSESSMENT OF AMERICAN SHAD FROM SELECTED ATLANTIC COAST RIVERS

October 1988



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PREFACE

This report was developed under the Atlantic States Marine Fisheries Commission's (ASMFC) Interstate Fisheries Management Program (ISFMP). The project was guided by the ISFMP Shad and River Herring Statistical and Scientific Committee with funds provided by NOAA-NMFS (Northeast Region) P.L. 89-304 project AFC, and P.L. 99-659 Interjurisdictional Grant NA 88EA-D-00066. Printing and distribution of the report was supported through U.S. Fish and Wildlife Service Federal Aid in Sport Fish Restoration administrative funds. ASMFC is especially grateful for the considerable contributions of time and expertise provided by the report authors from the States of Rhode Island, Connecticut and New York.

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Stock Assessment of American Shad From Selected Atlantic Coast Rivers

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Executive Summary

- 1) In this study, we used the Shepherd stock-recruitment (S-R) model to estimate maximum sustainable yield (MSY) and the maximum sustainable fishing rates (Fmsy) of 12 Atlantic coast shad stocks with long-term commercial catch-effort, age composition and mortality data. The current status of shad stocks was also assessed by comparing current fishing mortality estimates in each river to the Fmsy level. Finally, we examined to what extent clinal differences in MSY and Fmsy among the 12 shad rivers were related to life history and environmental properties of each spawning population.
- 2) The generalized Shepherd S-R model best described the stock-recruitment data in the Chowan River, North Carolina (r2=0.64), Delaware River (r2=0.521), Neuse River, North Carolina (r2=0.436), whereas the worst fits occurred for the Tar River, North Carolina (r2=0.110), St. Johns River, Florida (r2=0.144), Savannah (r2=0.223) and Altamaha (r2=0.224) rivers, Georgia.
- 3) Sustainable fishing rates (Fmsy) from the Shepherd model ranged from a low of 0.35 for the Pawcatuck River, Rhode Island to a high of 1.25 for the Chowan River, North Carolina. The overall mean Fmsy for all 12 shad stocks combined was 0.72 (95% CI: 0.56-0.87) which corresponded to a maximum harvest rate (Umsy) of 0.51 (95% CI: 0.40-0.62).

Given that the maximum harvest rates for 8 of the 12 shad rivers were below 0.60, these results suggest that it would be unwise to permit the maximum harvest rate of American shad to exceed 0.50 for a long period of time. This rate of exploitation applies only to stocks fully restored or those with relatively stable fisheries.

- 4) There was a distinct parabolic relationship between the sustainable fishing rates (Fmsy) and river latitude. Our results strongly suggest that American shad stocks at the northern (Pawcatuck and Connecticut rivers) and the southern (Altamaha and St. Johns rivers) edge of their range are less able to compensate for high (F>0.50) fishing mortality rates than are stocks near the center of their range.
- 5) The fishing mortality rates on American shad from the Susquehanna River during the mid-1970's greatly exceeded its maximum fishing rate, whereas recent fishing mortality rates in the Altamaha River are slightly above the Fmsy level. The current fishing rates for the other shad rivers were well below Fmsy levels.
- 6) The estimates of maximum sustainable yield (MSY) varied between a low of about 14,000 lbs for the Pawcatuck River, Rhode Island to a high of 2.7 million lbs for the Hudson River, New York. The magnitude of the MSY estimates among the 12 shad rivers was clearly related to the drainage area of each river.

- 7) The slope (a) at the origin of the Shepherd model, a measure of the stock's ability to tolerate exploitation, was generally highest among southern (south of Virginia) shad rivers, was positively correlated with population fecundity, and inversely related to river flow variability.
- 8) A linear multiple regression model, incorporating river latitude and flow variation, was developed to estimate sustainable fishing rates for rivers where stock assessment data were lacking. The model explained 82% of the variation in Fmsy and was validated using a jackknife procedure. In some cases where predictions were made (Cape Fear, Ogeechee), existing rates of fishing were similar to or greater than the predicted sustainable maximum.
- 9) The results suggest that southern shad rivers are more resilient to higher exploitation rates than northern rivers and, in some cases, can accommodate harvest rates beyond 0.60. Our Fmsy estimates, however, are subject to several sources of bias including measurement errors in the catch-effort and stock-recuitment data, poor precision about the Fmsy estimates, particularly from extreme northern (Kennebec and Penobscot) rivers that were outside the range of the predictive model, and random variability about the S-R models that were related to environmental effects on recruitment. Given these sources of bias, we strongly recommend that maximum harvest rates on American

shad, particularly from extreme northern and southern rivers, not exceed 0.50 for extended periods.

Introduction

The American shad, Alosa sapidissima, is the largest anadromous herring and spawns mainly during spring in many Atlantic coast rivers from Florida to Newfoundland (Walburg and Nichols 1967). These spawning runs are subject to commercial and sport fisheries of varying degree which currently account for about 90% of the total United States landings of American shad (ASMFC 1985). Total U.S. landings varied without trend (4-12 million pounds) from 1930 through 1970, but declined steadily thereafter to less than 4 million pounds by 1976, particularly from mid and south Atlantic rivers (ASMFC 1985). Although overfishing downstream of major spawning areas has been implicated as a major cause for this decline (Walburg and Nichols 1967; Crochet et al. 1976), no study has ever attempted to estimate historical fishing mortality rates on American shad over a wide temporal and spatial scale, and compare them to specific biological reference points such as F.01, Fmsy, or Frep (Sissenwine and Shepherd 1987). If the current fishing rates on American shad exceed such levels, then there would be a biological basis to conclude that growth and recruitment overfishing have occurred. A study of this type is necessary to assess the current status of Atlantic coast American shad stocks and to provide specific guidelines for developing management regulations on the commercial and sport fisheries.

There are major geographic differences in age at maturity, fecundity and postspawning natural mortality among shad stocks from Florida to Newfoundland which may affect stock stability and sustainable fishing rates (Leggett 1969). Shad stocks from northern latitudes (north of Chesapeake Bay) reach maturity later, are less fecund, and experience lower postspawning mortality than stocks found south of Virginia. Therefore, latitudinal variability in sustainable fishing rates (Fmsy) might be influenced by clinal differences in the life history parameters. Moreover, temporal variability in hydrographic conditions, such as river temperature and flow, tend to be more pronounced in rivers from northern latitudes (Leggett 1969). Since short-term fluctuations in river temperature and flow during the spawning period greatly influence year-class success of American shad (Marcy 1976; Crecco and Savoy 1987), it is also possible that clinal differences in temperature and flow variability might affect the ability of shad stocks to sustain higher exploitation rates. River morphometry factors (river length and drainage area) may also potentially affect stock stability, since shad population size is usually highest in large rivers, and stock abundance was shown to be positively correlated with Fmsy for a wide range of fish species (Garrod and Horwood 1984; Winters and Wheeler 1987; Lorda and Crecco 1987).

In this study we assessed the current status of American shad stocks using long-term commercial catch-effort, age

composition and mortality data for 12 Atlantic coast rivers ranging from Rhode Island to Florida (Figure 1). The objectives of this study were to: 1) estimate latitudinal changes in maximum sustainable yield (MSY) and the fishing rates at MSY (Fmsy) based on the stock-recruitment (S-R) properties of each stock, 2) determine the current status of each stock by comparing historical fishing rates in each river to the estimated Fmsy level, and 3) examine to what extent latitudinal variability in MSY and Fmsy is related to life history characteristics and environmental influences on each spawning population.

Methods

Data Sources- We conducted stock assessments for 12
Atlantic coast shad populations with commercial
catch-effort, population size, age structure, and mortality
data. Population dynamics studies were originally planned
for several other shad rivers such as the Potomac and
Nanticoke rivers in Maryland; the York, James, and
Rappahannock rivers in Virginia; the Cape Fear in N.
Carolina, the Waccamaw-Pee Dee in S. Carolina, and the
Ogeechee river in Georgia. However, the data sets from
these rivers were considered unreliable because the annual
catch-effort statistics either contained missing values,
were of short duration (< 15 years), or yielded imprecise
and implausible stock-recruitment parameters. A minimum
coefficient of determination (r2) of 0.100 for the S-R
model with a maximum coefficient of variation (CV) on the

slope parameter of 0.600, was required for inclusion in the assessment.

Relative stock size for 8 of the 12 rivers was expressed by long-term (15-50 years) catch-per-unit-effort (CPUE) data from commercial fishery records kept by the states or the federal government (Fisheries Statistics of the United States, 1934-1984), whereas annual stock sizes from the Connecticut, Pawcatuck, Delaware, and Altamaha rivers were based on population estimates (Crecco and Savoy 1987; Gibson and O'Brien 1988; Lupine 1986; Michaels 1987). Although sport fisheries for American shad exist on many Atlantic coast rivers (ASMFC 1985), long term (> 10 years) CPUE data for the recreational fisheries are available only for the Connecticut River. Therefore, recreational catch-effort data were not used in this analysis.

The ability to discern long-term trends in stock abundance with CPUE data depends on the assumption that changes in CPUE are directly proportional to annual population changes. This implies that the catchability coefficient, or the percentage of the exploitable stock removed by each unit of fishing effort, remains constant or independent of stock size. This assumption may not hold entirely for some commercial shad fisheries, given that Crecco and Savoy (1985) found that the catchability coefficient for the commercial shad fishery in the Connecticut River was inversely related to stock size. They concluded that commercial gill net fishermen do not fish randomly, but instead set their nets where and when the probability of catching shad is highest. As a result,

commercial CPUE data tend to underestimate true fluctuations in stock size. The problem is likely to be most severe in "search" type fisheries (drift gill nets) as opposed to fixed gears (staked gill net, pound net).

Despite this intrinsic bias, we agree with the conclusions of other studies (Koo 1970; Klauda et al 1976; Summers and Rose 1987) that pronounced trends in stock abundance are reflected accurately by long-term (20-40 years) commercial CPUE.

Annual commercial landings from all rivers were expressed in pounds, whereas fishing effort was represented in several ways depending on the quality of the effort data sets. The most accurate and comprehensive effort statistics are from the Connecticut, Hudson, and Altamaha rivers (Crecco and Savoy 1987; Klauda et al 1976; Michaels 1984); where annual fishing effort was the total number of days fished by the principle gear types (number or linear yards of drift or stake gill nets, pound nets and haul seines) known to harvest shad. To calculate total annual fishing effort (Et) for these rivers, the number of days fished by each gear was converted to equivalent fishing effort units by scaling the days fished using the long-term average CPUE for each gear (Klauda et al 1976; Leggett 1976). Annual fishing effort for the Delaware River was represented by a relative effort index (Erel):

Erel= Ct/CPUE (1)

where: Ct is the annual commercial landings (Art Lupine pers comm) and CPUE is the corresponding mean annual catch per seine haul from the Lewis haul seine fishery (Chittendan 1969; Lupine 1986). Annual fishing effort for all other rivers was the product of the number of licensed fishing gear or linear yards known to catch shad multiplied by the average days fished by each gear (Talbot 1954; Fredin 1954). Statistics on licensed gear are a somewhat crude measure of fishing effort since a license issued for each gear provides no information whether and to what extent that gear was fished during each year.

Stock-Recruitment Data- A time series of adult shad population estimates (Nt) in weight (lbs.) for each river was taken from published studies (Michaels 1984; Crecco and Savoy 1987; Lupine 1986; Gibson and O'Brien 1988); or was reconstructed with Leggett's (1976) equation:

$$Nt = Ct/(1-exp(-q*Et)) , \qquad (2)$$

which utilizes commercial catch (Ct) and effort (Et) data, and where q is the average commercial catchability coefficient from each river. The q for several rivers was estimated directly from published tag (Mt) and recapture (Rt) studies (Table 1):

$$q = Rt/(Mt*Et). (3)$$

Corrections were made where necessary for the use of disc tags which increase the vulnerability of tagged shad to recapture (Leggett 1976). The long-term mean q for each river was computed from the annual q values from each tag-recapture study.

In certain rivers, no tag-recapture studies were ever conducted, so q was estimated by dividing the instantaneous fishing mortality rate (Ft) for each year by the corresponding fishing effort (Et):

$$q = Ft/Et$$
 (4)

or by a surplus-production model that explicitly estimates q from annual catch (Ct) and effort (Et) data (Jensen 1986):

Ct=
$$q*Et*B-(q^2*B/K)*Et^2$$
. (5)

Instantaneous fishing rates to be used in equation (4) were estimated in the following way: 1) total instantaneous mortality rates (Z) were determined by catch curve analysis of the age and spawning frequencies (Crecco and Gibson 1987) from various studies (Table 1), and 2) the long-term average natural mortality rate (M) for adult shad was determined from each river either directly from age structure and spawning frequency data (Leggett 1976), or indirectly, using the methods of Pauly (1980) and Hoenig (1983). Since total mortality (Z) is the sum of fishing (F) and natural (M) mortalities, the fishing rate can be

obtained by subtraction. It should be pointed out that all shad stocks from rivers between South Carolina and Florida die after spawning, so that post-spawning natural mortality approaches 100%. Therefore, equation (4) and catch curve analysis were only applied to shad stocks (north of the Cape Fear River, N. Carolina) where significant post-spawning survival takes place (Leggett 1969).

The annual weight (lbs.) of the spawning stock (Pt) in each year was the annual population estimate (Nt) minus that year's commercial catch (Appendix 1). Since American shad generally mature between ages 3 and 6 (Leggett 1969), total recruitment (lbs.) of virgin shad from each year-class was the sum of virgin 3,4,5, and 6 year old shad in the t+3, t+4, t+5, and t+6 spawning runs (Nt), based on either average age-specific maturation rates from each river or long-term age structure and spawning history data. Although this method of estimating recruitment does not explicitly account for density-dependent changes in maturation, data on age-specific maturation by year-class were used when such information was available (i.e. Connecticut and James rivers). Shad recruitment (Rt) from each river (Appendix 1) was expressed in numbers by dividing the total weight of recruits by the average weight (lbs.) of a first-time spawner. Unlike the other rivers, the final recruitment estimates for the Delaware River were based on the mean juvenile indices monitored annually from 1971 through 1986 (Lupine 1986) scaled to the corresponding adult recruitment estimates.

Stock-Recruitment Model- A knowledge of the stock-recruitment (S-R) characteristics of exploited fish stocks is becoming increasingly important in determining safe long-term fishing rates and maximum allowable yields (Cushing and Harris 1973; Garrod 1982). The problem of selecting fishing rates that not only maximize yield, but also ensure a viable spawning population, was explored with a steady-state model developed by Shepherd (1982). This model predicts equilibrium commercial yields (lbs.) for American shad with changes in commercial fishing mortality (F) by combining the results of yield-per-recruit (Y/R) and biomass-per-recruit (B/R) analyses with the stock-recruitment properties for each stock.

The Thompson-Bell yield model (Thompson and Bell 1934) was used to generate Y/R and B/R values for each shad stock (sexes combined) over a range of fishing mortality rates (F=0.10-1.30 at 0.10 increments). For each model run, the natural mortality rate (M) was held constant for all age groups at the river-specific levels for rivers north of the Neuse River, N. Carolina, or at 5.0 for rivers from S. Carolina to Florida, where post-spawning mortality approaches 100%. For each river, age-specific growth in weight (lbs.) (sexes combined) was expressed either by von Bertalanffy growth equations or by published age-weight relationships. In the model, each fish was allowed to recruit to the spawning population according to the average age-specific maturation rate for that river.

After Y/R and B/R values were generated, American shad recruitment in numbers (Rt) and spawning stock (Pt) for

each river (Appendix 1) was fitted to the Shepherd (1982) stock-recruitment model:

$$Rt=a*Pt/[1+(Pt/K)^B], (6)$$

where: a= the slope of the S-R curve at the origin, B= a shape parameter and measure of density-dependent mortality, and K= spawning stock size at which density-dependent effects dominate. The estimates of a, B, and K and their standard errors (SE) were determined by nonlinear least squares regression (SAS 1985). The relative precision about each parameter estimate was based on the coefficient of variation (CV=SE/mean). The shepherd model is potentially very versatile because it can be fitted to power, asymptotic, and dome-shaped S-R curves. The major limitation of the Shepherd yield model, as with all S-R models, is demonstrating the precision and accuracy of the parameters (a,B,K), particularly the slope at the origin (a), which greatly affects the magnitude of Fmsy and MSY.

Having estimates of Y/R, B/R, and the S-R parameters (a,B,K), the equilibrium spawning stock biomass (P) expected at each fishing rate (F) was estimated by substituting the corresponding B/R value for each F into the rearranged Shepherd model:

$$P = K(a*(B/R)-1)^1/B.$$
 (7)

The corresponding equilibrium recruitment (R) at each F was expressed by:

$$R = P/(B/R) \tag{8}$$

and the predicted equilibrium commercial yield (Y) was the product of shad recruitment (R) times the corresponding Y/R value:

$$Y = R * Y / R. \tag{9}$$

In these analyses, the maximum sustainable yield (MSY) was represented by the peak of the equilibrium yield curve, whereas Fmsy was the fishing rate at which MSY takes place. The percentage harvest (Umsy) that corresponded to the instantaneous rate (Fmsy) was expressed by:

$$Umsy=1-exp(-Fmsy). (10)$$

To determine whether overfishing has occurred for each shad stock, we estimated the historical commercial fishing rates (Fhist) experienced by shad in each river:

$$Fhist = q*Et, (11)$$

where: q is the river-specific catchability estimate (Table 1). We then compared the time series of Fhist values to the corresponding Fmsy, and if overfishing occurred in the past, some of the Fhist values would exceed Fmsy. We also estimated the current mean fishing mortality rate (Fcur) experienced by shad in each river based on equation (11),

and the most recent five years of effort data (Et). In the case of the Susquehanna River, fishing effort data were lacking after 1978, so that the current fishing mortality rate (Fcur) was based on the 1973-1978 data. If Fcur for any river exceeded its Fmsy value, then our analysis would suggest that recruitment overfishing is currently taking place in that river.

Life History and Climatic Effects on Fmsy-In this analysis, we assumed that the shad stocks with higher Fmsy levels were more stable and better able to compensate for higher exploitation rates. To determine whether changes in life history factors, river morphometry and abiotic factors could affect sustainable fishing rates, we used multiple linear regression analysis (Draper and Smith 1982) to relate the Fmsy estimates for the 12 shad rivers to several life history (fecundity, average historical yield and river latitude), river morphometry (river length and drainage area) and abiotic factors (mean river flow and the coefficient of variability (CV) about river flow). River latitude was considered to be related to the life history of American shad because Leggett and Carscadden (1978) demonstrated that certain life history factors such as fecundity, age at maturity, and natural mortality vary in a north-south direction. The latitude of each river was measured (minutes north to south) from an Atlas of state maps.

Mean population fecundity (eggs per pound) was expressed by dividing the average fecundity of each stock by the

average weight of a female spawner derived from several studies (Lehman 1953; Davis 1957; Leggett and Carscadden 1978). The historical average yield (lbs) for each river was determined from commercial landings between 1895 and 1905 (Walburg and Nichols 1967). Since water pollution and fishing pressure were presumably much lower in 1895 then the present, these historical landings were considered to be a relative measure of potential fish productivity among the 12 stocks.

The morphometric factors, such as river length (miles) and drainage area (sq miles), were estimated from state maps and from data supplied by the United States Geological Survey (USGS). The abiotic factors consisted of annual mean and variability (CV) among monthly river flows (m3/sec) which were represented by USGS flow data for the last 10 years.

The Fmsy values from the Shepherd S-R model were related to the life history, morphometric and abiotic variables (X1 to X3) in a linear regression model:

$$Fmsy = b0+b1(X1)+b2(X2)+b3(X3)$$
 (12)

where: b0, b1, b2, and b3 are parameters to be estimated. Equation (12) was fitted to the data by the maximum r-square procedure (SAS 1985), where a maximum of three predictor (Xi) variables was included due to the small number of degrees of freedom (12 shad rivers) available. The statistical criterion for selecting any of the factors was set at the probability level P<0.05. Given the

relatively small data set and the possibility that serial correlations were present among the predictor variables (Xi), we used jackknife and cross-validation methods (Miller 1974; Efron 1982) to estimate the magnitude and direction of bias in predicting Fmsy for each river. The jackknife method involves predicting Fmsy with equation (12) for each river without including the predictor variables (Xi) for that river. This process is repeated so that n sets of partial estimates (based on n-1 observations) are available to compute the final parameter estimates (b0, b1, b2, b3) and their standard errors (SE). To complete the cross-validation procedure, the Fmsy values from the Shepherd model (equation 6) were linearly regressed against the jackknife estimates of Fmsy (now independent). The model validation portion of the analysis was considered complete if the estimates of the slope and intercept did not differ significantly (P<0.05) from 1.0 and 0, respectively.

If the multiple regression model (equation 12) predicted Fmsy with high precision for the 12 American shad stocks, realistic estimates of Fmsy would be possible for other shad rivers (i.e. James, Ogeechee and Potomac rivers) where stock-recruitment data were shown to be lacking or unreliable. Therefore, we attempted to estimate sustainable fishing rates (Fmsy) for those rivers by substituting their respective life history and abiotic factors (Xi) into equation (12).

Stock-Recruitment Properties of Each Stock-The degree of fit (r2) of the generalized Shepherd S-R model to observed stock-recruitment data (Appendix 1) was highly variable from the 12 shad rivers (Table 2; Figures 2-13). The S-R fits for all 12 stocks reached the minimum r2 criterion of 0.10 (range: 0.11-0.62). There was no apparent latitudinal pattern in the magnitude of the r2 values among the 12 stocks. The Shepherd S-R model best described the stock-recruitment data in the Chowan (r2=0.624), Delaware (r2=0.521) and Neuse (r2=0.436) rivers, whereas the worst fits occurred in the Tar (r2=0.11), St. Johns (r2=0.144), Savannah (r2=0.223) and Altamaha (r2=0.224) rivers. The fact that spawning stock size usually explained less than 40% of the recruitment variability is not surprising, given the potential measurement error in the data, and the acknowledged importance of density-independent factors in affecting recruitment variability.

The relative precision about the Shepherd S-R parameters varied greatly among the 12 shad stocks (range: 0.10-1.41), but more reliable (low CV values) estimates were found generally in shad rivers north of the Tar River, North Carolina (Table 3). Except for the St. Johns river, the CV values about the slope parameter for all other rivers were less than 0.60. Exceptionally high precision for all three parameters (a, B, K) was evident for the Chowan River, North Carolina, as well as for the North Atlantic shad rivers (Pawcatuck, Connecticut and Hudson rivers). The relative precision of the S-R parameters for the St. Johns,

Susquehanna and Edisto rivers was poor and was only included here to provide a relative comparison between northern and southern shad rivers.

The shape of the predicted S-R curves among the 12 Atlantic coast shad stocks varied from flat-topped (asymptotic) to dome-shaped (Figure 2-13). For shad stocks not fully restored, such as the Pawcatuck (Figure 2) and Delaware (Figure 5) rivers, a pronounced ascending limb was observed with many points close to the origin. By contrast, certain American shad stocks close to equilibrium, such as the Connecticut and Savannah rivers, had most of the S-R points near the center of the distribution. As a result, their S-R curves were fairly dome-shaped with a clear descending limb (Figures 3 and 11). Three rivers (Chowan, Edisto and Altamaha) showed a wide distribution of stock-recruitment points that were also well approximated by dome-shaped (Ricker-type) S-R curves (Figure 7, 10, and 12). The Neuse was the only shad river where the S-R points were distinctly asymptotic (Beverton-Holt type) (Figure 9). For the remaining stocks (Hudson, Susquehanna, Tar, St. Johns), the S-R points were widely scattered and poorly described by the Shepherd or any other S-R model. This may have occurred either because of significant measurement errors of the stock and recruitment estimates, or because shad recruitment variability among these rivers was more dominated by density-independent (climatic) factors.

Biological Reference Point (Fmsy)-Estimates of the sustainable fishing rates (Fmsy) from the Shepherd model

ranged from a low of 0.35 (Umsy=0.30) for the Pawcatuck River, Rhode Island to a high of 1.25 (Umsy=0.71) for the Chowan River, North Carolina (Table 4). The overall mean Fmsy for all 12 shad rivers combined was 0.72 (95% CI: 0.56 to 0.87) which corresponded to a maximum harvest rate (Umsy) of 0.51 (95% CI: 0.40 to 0.62). Given that the maximum harvest rates (Umsy) for 8 of the 12 shad rivers were below 0.60, these data suggest that it would be unwise to permit the harvest rate of American shad to exceed 50% of adult stock (both sexes) for long periods of time.

The mean fishing rate (Fcur=0.94) experienced by American shad in the Susquehanna River during the 1970's greatly exceeded its Fmsy estimates (Table 4), implying that overfishing was a major cause of the American shad stock collapse in that river during the late 1970's. The recent fishing mortality rate (Fcur=0.57) on American shad in the Altamaha River was slightly above the Fmsy level of 0.55, whereas the current fishing mortality rates in the other 10 rivers were well below Fmsy levels.

Although sustainable fishing rates (Fmsy) were highly variable among the 12 Atlantic coast rivers, there was a distinct parabolic relationship between Fmsy and river latitude (Table 4; Figure 14). The mean estimates of Fmsy rose steadily from the Pawcatuck River, Rhode Island (Fmsy=0.35) to a maximum (Fmsy=1.25) for the Chowan River, North Carolina, then declined fairly steadily thereafter, especially for the extreme southern rivers (Altamaha and St. Johns rivers). These data strongly suggest that American shad stocks at the northern and southern edge of

their range are less able to compensate for high (U>0.50) exploitation rates than are stocks near the center of their range.

The estimates of maximum sustainable yield (MSY) varied between a low of about 14,000 lbs for the Pawcatuck River, Rhode Island to a high of 2.7 million lbs for the Hudson River, New York (Table 4). The magnitude of the MSY estimates among the 12 shad rivers was clearly related to river drainage area, insofar as the two highest MSY estimates occurred in the two largest shad rivers: the Hudson and the Susquehanna rivers. Except for the Delaware, the MSY estimates for the other 11 rivers were positively correlated (r=0.85, P<0.01) to the mean historical landings from that river between 1895 and 1905 (Table 4; Figure 15). This indicated that our MSY estimates are a reasonable measure of potential yield for most shad rivers.

process related to Stock Stability-The slope (a) at the origin of the Shepherd model, a measure of the stock's ability to tolerate exploitation (Figure 16), showed clinal differences among the 12 shad rivers and were correlated with certain life history and abiotic factors. The magnitude of the (a) values was generally highest among southern (south of Virginia) shad rivers (Table 2), was positively correlated with population fecundity (r=0.371, P<.036) (Figure 17), and was inversely related (r=0.841, P<.01) to river flow variability (Figure 18). Our results suggest that shad stocks from mid-Atlantic rivers can generally accommodate higher sustainable fishing

mortalities than northern rivers because these shad stocks evolved a suite of life history traits (high fecundity, shorter life span and early maturation) that can adapt to more stable environmental conditions.

A three factor regression model, consisting of latitude (Figure 14), latitude squared, and relative flow variation (Figure 18) was the best predictive model, explaining 82.3% of the variability in the sustainable fishing rates (Fmsy) for the 12 shad stocks (Table 5). The mean squared error about the predicted values was on the order of Fmsy +0.27. This represented about a 30% error which we felt was acceptable for predicting preliminary Fmsy estimates for other shad stocks. Results of the jackknife and cross-validation procedures (Table 6) revealed that the multiple regression model predicted sustainable fishing rates (Fmsy) for the S-R models with high precision (maximum deviation=0.138). The independent observed and predicted Fmsy values were also highly (r=0.78, P<0.01) correlated (Figure 19), indicating that the multiple regression model is a reasonably good predictor of Fmsy. Using the jackknife procedure, the overall mean harvest rate (U) among the 12 rivers was 0.55 (95% CI:0.40-0.65), which is regarded as the most reliable estimate of a coast-wide maximum harvest rate.

Having data on river latitude and flow variability for 12 other shad rivers located from Maine to Georgia, the multiple regression model (Table 5) was used to predict sustainable fishing rates (Fmsy) for those rivers (Table 7). Note that the range of predicted Fmsy estimates (range:

0.21 to 1.44) for the additional rivers was wider than that (range: 0.39 to 1.21) for the original 12 shad rivers (Table 6). This is because many of the additional rivers were chosen from the extreme northern (Penobscot and Kennebec rivers, Maine) or mid-southern range (York, James and Roanoke rivers) for American shad. Current fishing rates in the Cape Fear River exceeded the predicted Fmsy while fishing rates in the Ogeechee River during the early 1970's exceeded its predicted Fmsy. The Ogeechee is now open only two days per week as a result of this overfishing.

Discussion-

We were able to estimate sustainable fishing rates (Fmsy) with the Shepherd (1982) S-R model (Table 2) with varying degree of success. The shape of the S-R curves, which is primarily controlled by the B parameter, was highly variable (Figures 2-13). Shepherd (1982) hypothesized that the B parameter should be fairly constant among fish populations with similar life histories. Our estimates of B among the 12 rivers ranged widely from 1.229 to 4.808. When only the more precise estimates are considered, the range is still considerable (1.229-3.092), although some of the variability in B is undoubtedly due to the range of spawning stocks in the S-R data. Our results suggest that the B parameter is not constant, but varies among stocks of American shad. Apparently, shad exibit stock-specific levels of compensation, but the underlying mechanisms are

still unclear. We could find no statistical relationship between the B estimates and the biotic, abiotic, and morphometric variables available in this study. Our results are similar to those of Winters and Wheeler (1987) who found considerable variation (including a latitudinal affect) in compensatory ability among stocks of spring-spawning herring (Clupea harengus). Variability in stock-recruit parameters also occurs in chinook salmon (Onchorynchus tshawytscha), leading to differences in sustainable fishing rates (Hankin and Healey 1986) for this species.

Our estimates of Fmsy are highly sensitive to the slope parameter (a) in the S-R model. The significant correlations between the (a) parameters and fecundity and between (a) and flow variability, have clear underlying biological and physical mechanisms. Since alpha measures the absolute rate of recruitment per unit spawner in the absence of density-dependent effects, those stocks that produce more eggs per pound of spawner should generate more recruits. Therefore, the significant positive correlation between relative fecundity and the (a) estimates is consistent with this hypothesis. The significant inverse relationship between the (a) estimates and flow variability suggests that density-independent mortality rates are higher in shad stocks subject to episodic storm events that cause high river flow variability.

The parameter K in the Shepherd model is the level of spawning stock at which density-dependent mortality begins to dominate and, as such, is related to environmental

carrying capacity. Although the positive correlation between K and river drainage area (p=0.069) was not quite significant, large drainage areas are generally associated with bigger populations making this marginal correlation logical. We were also able to correlate our estimates of MSY with historical catch records. It was necessary to drop the Delaware River, an outlier, to achieve the correlation. Yields in the Delaware River at the turn of the century greatly exceeded that for any other shad river, approaching 20 million pounds. Extraordinary pollution problems (Sykes and Lehman 1957) considerably reduced this river's productive ability. Excluding the Delaware, estimated MSY showed a strong linear relationship with average reported catches during the period 1895-1905. Of interest is the slope of the fitted regression, 0.734, which suggests that current sustainable yields will be less than historical catches. Collectively, these correlations of important parameter estimates with independent data sources indicate that our analyses have effectively captured the paramount S-R properties of the various stocks.

Our analyses suggest that American shad exhibit density-dependent stock and recruitment, the degree of which appears to be river-specific. Consequently, sustainable fishing rates also vary. When the stock and recruitment properties of each stock are coupled with yield per recruit models, these S-R functions indicate that fisheries may harvest from 30 to 70% of the adult stock in a population. The higher fishing rates are associated with populations near the center of the species range that are

exposed to low river flow variability. As a consequence, shad populations at the limits of the species range should be fished more conservatively. These models are deterministic and the Fmsy values apply only to stocks that are fully restored or which have supported long-term fisheries. This caveat is noteworthy, given that certain stocks (Pawcatuck, Delaware, Susquehanna, and Ogeechee) are currently depleted and should not be fished at estimated Fmsy levels. Moreover, because of short-term changes in recruitment due to variability in environmental factors, the MSY and Fmsy values given in this study should be considered long-term averages. No attempt has been made to estimate confidence limits on our estimates of Fmsy through say, propagation of error (first-order analysis) techniques (Lettenmaier and Richey 1979) or jackknife procedures (Tukey 1977). Since there are measurement errors in stock-recruitment data (Walters and Ludwig 1981) and subtle time series biases introduced by fitting methods (Walters 1985), more conservative levels of fishing should be chosen until variance estimates and these sources of bias can be addressed. Walter's (1985) simulation studies with Pacific salmon suggested that sustainable exploitation rates could be overestimated by as much as 30%. In the absence of better information, we recommend that rates of exploitation on shad populations (both sexes) not exceed 50% for extended periods of time

Estimation of maximum fishing rates is only half of the information needed for effective shad management. More reliable estimates of current exploitation rates are

needed, particularly in the rivers where our estimates of current rates exceeded the suggested Fmsy level. We further recommend that coastal states implement programs to periodically determine annual fishing rates. Several methods exist to estimate F (Crecco and Gibson 1987). It should be remembered that for southern shad stocks with no repeat spawning, tagging studies are the only method by which fishing rates may be estimated. More precise estimates of stock-recruitment data should also be obtained. Methods to filter environmental effects from the S-R data (Crecco and Savoy 1987; Welch 1987) can be used to obtain more precise estimates of the important slope parameter (a).

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Table 1 Average estimates of the catchability coefficient (q) by river system for the commercial shad fishery based on several methods.

River	Mean Catchability Coefficient	Method		
Pawcatuck River Rhode Island	Unknown	No Commericial Fishery		
Connecticut River Connecticut Massachasetts	1.8 x 10 ⁻⁴	Based on 1966-73 and 1977-80 tag- recapture studies (Leggett 1976; Minta 1980)		
Hudson River New York	3.5 x 10 ⁻⁵	Based on 1950-51 tag-recapture study (Talbot 1954)		
Delaware River Delaware New Jersey	8.3×10^{-5}	Based on the average of the 1975-86 tag-recapture studie (Lupine 1986)		
Susquehanna River Maryland Pennsylvania	1.8 x 10 ⁻⁶	Based on 1951 tag-recapture study (Walburg 1955)		
Nanticoke River Delaware	8.3 x 10 ⁻⁶	Estimated indirectlusing fishing effor in Nanticoke River in 1951 plus the mark-capture Festimates in Chesapeake Bay (Walburg 1955)		

Table 1 continued

James River	-5	Based on 1954 tag-
Virginia	2.0 x 10 ⁻⁵	recapture study (Walburg and Skyes 1957) and 1977-80 catch curve analysis (Bruce Hill pers comm) with natural morality (M) = 1.4 by Hoenig (1983) method
Chowan River North Carolina	1.1 x 10 ⁻⁶	Based on 1977-79 catch curves (Harrell Johnson pers comm) with natural mortality (M) = 1.7 by Hoenig (1983) method
Tar-Pamlico River North Carolina	3.2×10^{-5}	Based on 1983-84 catch curves (Harrell Johnson pers comm) with natural mortality (M) = 1.7 by Hoenig (1983) method
Neuse River North Carolina	1.4×10^{-6}	Based on 1951 tag-recapture study (Walburg 1953)
Edisto River South Carolina	4.1×10^{-4}	Based on tag- recapture study (Walburg 1956)
Savannah River Georgia	1.0×10^{-4}	Surplus Production Model of Jensen (1986)
Altamaha River Georgia	1.7×10^{-4}	Average of the 1967-68 and 82-86 tag-recaptuare studies (Goodwin 1968; Michaels 1987)

Table 1. Average estimates of the catchability coefficient (q) by river system for the commercial shad fishery based on several methods.

River	Mean Catchability Coefficient	Method
Ogeechee River Georgia	4.02×10^{-4}	Based on tag-recapt- ures, Sykes 1956
St. John's River Florida	3.5×10^{-4}	Based on 1953-1958 tag-recaptures,Wal- burg 1960

Table 2. Estimates of the Shepherd stock-recruitment parameters (a,B.K) for 12 shad rivers and their standard errors (parenthesis). r^2 is the coefficient of determination.

River	S-R-	Parameters		2
7	a	B	К	r
Pawcatuck ¹ /	0.448(0.137)	2.363	80000	0.350
Connecticut	0.506(0.141)	2.779(0.986)	1326000(326200)	0.272
Hudson	0.482(0.102)	2.422(1.408)	4389000(889300)	0.350
Delaware	0.776(0.204)	2.217(1.340)	822883(297045)	0.521
Susquehanna	0.779(0.449)	1.624(1.019)	1945000(1515000)	0.381
Chowan	1.243(0.137)	3.092(0.538)	163836(16208)	0.624
Tar	1.009(0.373)	2.582(1.296)	286258(100701)	0.106
Neuse	1.551(0.818)	1-229(0.409)	225600 (196600)	0.436
Edisto	0.844(0.349)	4.808(6.286)	169100(81810)	0.288
Savannah	1.522(0.638)	1.808(0.424)	164010(76810)	0.223
Altamaha	0.670(0.243)	2.362(0.969)	120100(53590)	0.224
St. Johns	1.045(0.974)	1.398(1.251)	1534000(2157000)	0.144
Means	0.9079	2.393	1013253	0.327

 $^{1\ /\}$ Only ascending limb of S-R model estimated, B value is mean of other rivers, K based on river drainage area

Table 3 Coefficient of variation (CV) about the Shepherd S-R parameters (a, B, K) for each of the 12 shad rivers. Coefficient of variability was computed for each parameter estimate as the standard error divided by the mean from Table 2.

S-R Parameters								
River	a	В	K	Geometric Mean				
	Co	efficient of	Variation					
Pawcatuck	0.31	-	-	0.31				
Connecticut	0.28	0.35	0.25	0.29				
Hudson	0.21	0.58	0.20	0.29				
Delaware	0.26	0.60	0.36	0.38				
Susquehanna	0.56	0.63	0.78	0.65				
Chowan	0.11	0.17	0.10	0.12				
Tar	0.37	0.50	0.87	0.54				
Neuse	0.53	0.33	0.87	0.53				
Edisto	0.41	1.31	0.48	0.64				
Savannah	0.42	0.23	0.47	0.36				
Altamaha	0.36	0.41	0.44	0.40				
St.Johns	0.93	0.89	1.41	1.05				

Table 4. Estimates of maximum sustainable yield (MSY), F_{msy} , % of harvest(Umsy), F_{hist} , and historical yields for 12 shad rivers.

River	F _{msy}	Umsy	MSY(1bs)	F _{hist}	MSY _{hist} (lbs.)
Pawcatuck	0.350	0.295	14031	0.008	17850
Connecticut	0.500	0.393	531000	0.151	445500
Hudson	0.600	0.451	2722128	0.375	2937385
Delaware	0.795	0.548	651500	0.320	5757000
Susquehanna	0.700	0.503	1342000	0.942	2500000
Chowan	1.250	0.713	282100	0.675	604043
Tar	1.030	0.643	340000	0.794	220662
Neuse	1.000	0.632	430874	0.641	681084
Edisto	0.800	0.551	136317	0.135	103586
Savannah	1.120	0.674	261000	0.416	302220
Altamaha	0.550	0.423	288640	0.573	233890
St. Johns	0.600	0.451	768928	0.090	1100642
Means	0.716	0.511			
SE	0.078	0.056			

Table 5. Multiple regression model to predict ^Fmsy for 12 Atlantic shad rivers, as well as parameter estimates and their standard errors.

Model
$$F_{msy} = b_0 + b_1 \text{ (lat)} + b_2 \text{ (lat}^2) + b_3 \text{ (Flow CV)}$$

Where: F_{msy} = Fishing rate at MSY;

Lat = Latitude(degrees)of river mouth

Flow CV = Coefficient of variation about mean river flow

<u>Parameter</u>	<u>Estimate</u>	<u>SE</u>	<u>t-statistic</u>	P/b = 0
b _o	-18.2630	-	4	-
b ₁	0.0183	0.0057	3.53	0.008
b ₂	- 0.0000042	0.0000012	-3.50	0.008
b ₃	-0.6986	0.4262	-1.64	0.140

$$r^2 = 0.823$$

MSE = 0.01846
SE of Reg. = 0.1359

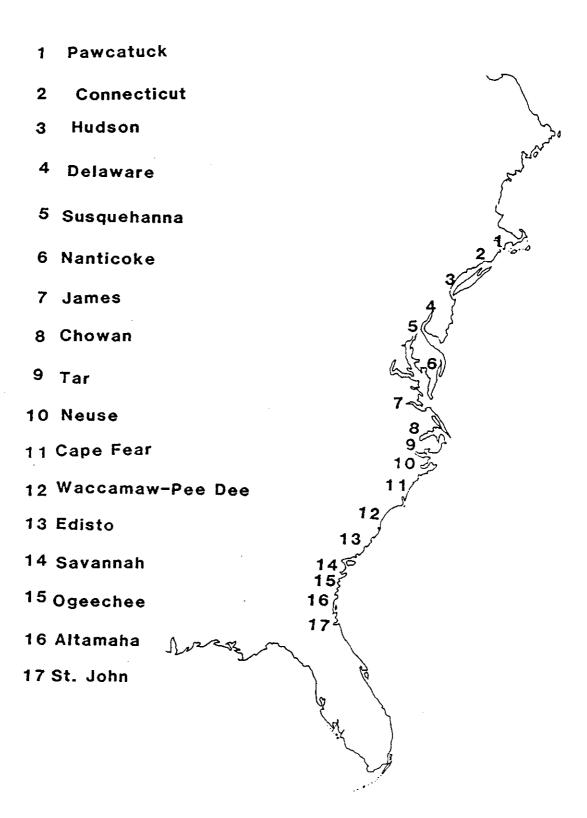
Table 6. Results of jackknife and cross-validation procedures for the multiple regression model to predict $F_{\mbox{msy}}$ for 12 Atlantic coast shad stocks

River	Assessed F _{msy}	Predicted F _{msy}	Deviation	SE Reg.	95% CI
Pawcatuck	0.350	0.409	-0.059	0.144	0.121 - 0.697
Connecticut	0.500	0.385	0.115	0.141	0.103 - 0.667
Hudson	0.600	0.636	-0.036	0.145	0.346 - 0.926
Delaware	0.795	0.857	-0.062	0.145	0.567 - 1.147
Susquehanna	0.700	0.765	-0.065	0.145	0.475 - 1.055
Chowan	1.250	0.889	0.361	0.093	0.703 - 1.075
Tar	1.030	1.209	-0.179	0.137	0.935 - 1.483
Neuse	1.000	1.210	-0.210	0.132	0.946 - 1.474
Edisto	0.800	0.875	-0.075	0.143	0.589 - 1.161
Savannah	1.120	0.858	0.262	0.115	0.628 - 1.088
Altamaha	0.550	0.752	-0.202	0.135	0.428 - 1.022
St. Johns	0.600	0.628	-0.028	0.145	0.338 - 0.918
Means	0.775	0.789	-0.015	0.135	0.519 - 1.060

Table 7. Predictions of sustainable fishing rates (Fmsy, msy) for several other shad rivers along the Atlantic Coast from the multiple regression model

River	Fmsy	Umsy	95% CI on Fmsy	Fcurr
Penobscot	0.212	0.200	0 - 0.484	-
Kennebec	0.446	0.360	0.175 - 0.718	-
Merrimac	0.599	0.451	0.327 - 0.871	-
Potomac	1.158	0.686	0.886 - 1.430	0.951
Nanticoke	0.985	0.627	0.714 - 1.257	0.799
Choptank	0.907	0.596	0.636 - 1.179	-
York	1.231	0.708	0.959 - 1.503	0.755
James	1.280	0.722	1.008 - 1.552	0.884
Roanoke	1.436	0.762	1.164 - 1.708	-
Cape Fear	1.311	0.730	1.039 - 1.582	1.657
Waccamaw-Pee	1.260	0.716	0.998 - 1.532	0.690
Dee Ogeechee	1.062	0.654	0.790 - 1.335	0.966

Figure 1- EAST COAST SHAD RIVERS Examined in Stock Assessment



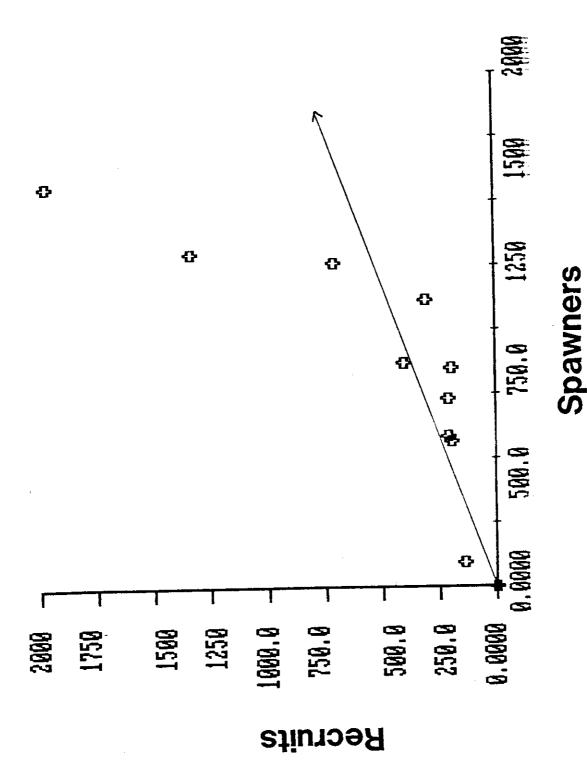


Figure 2 Pawcatuck River S-R Plot

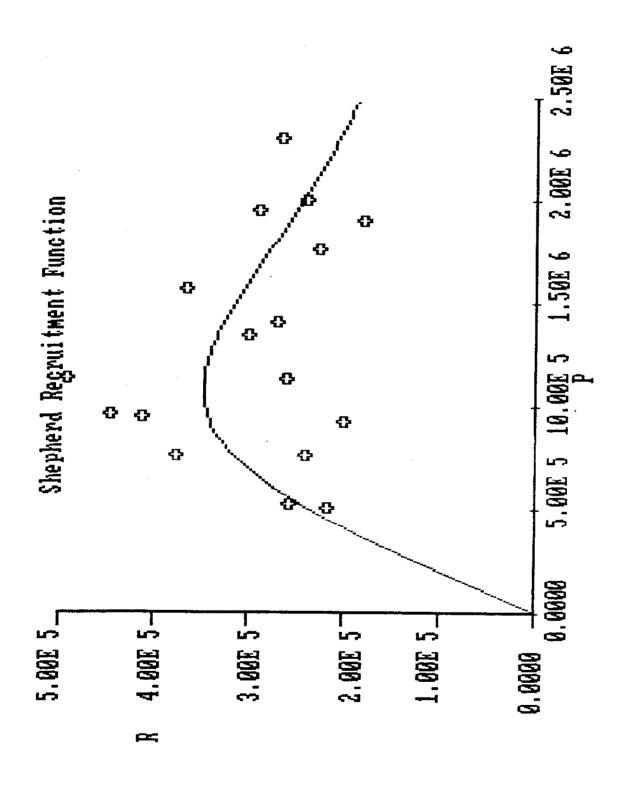


Figure 3- Connecticut River S-R Plot

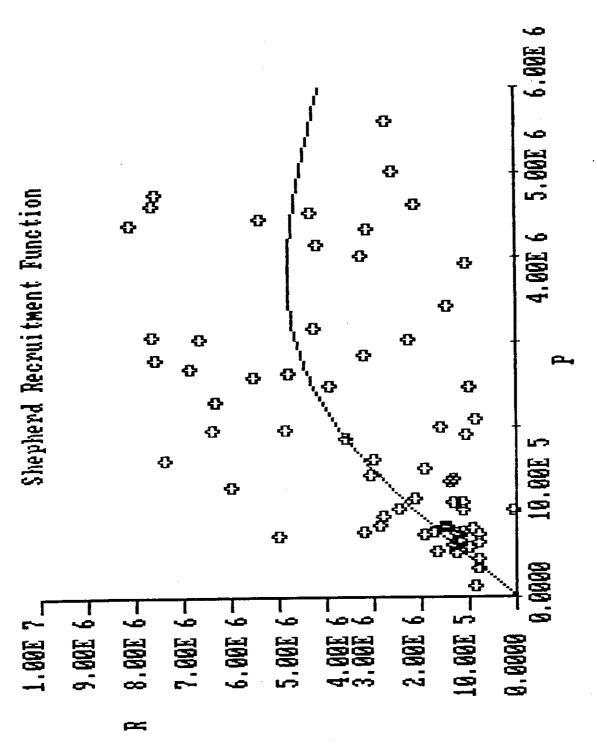
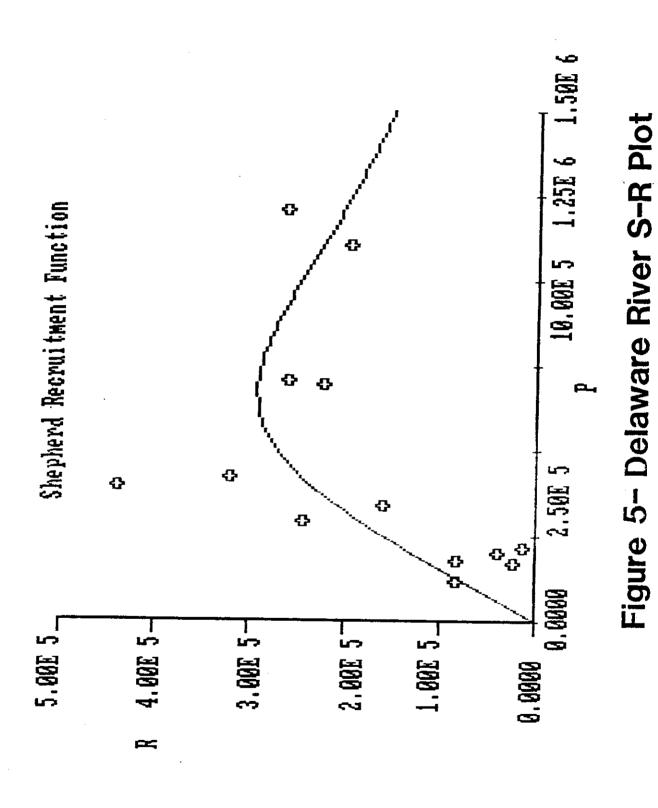
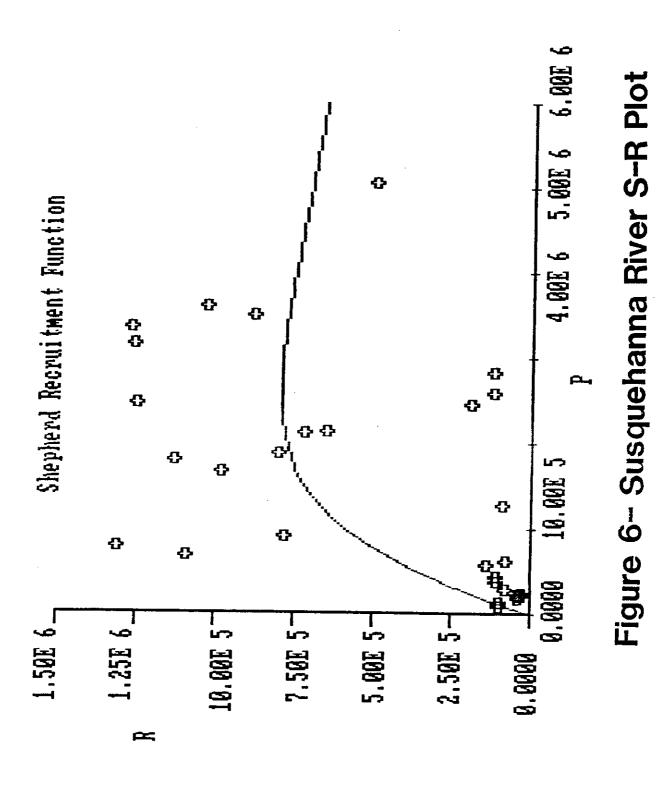
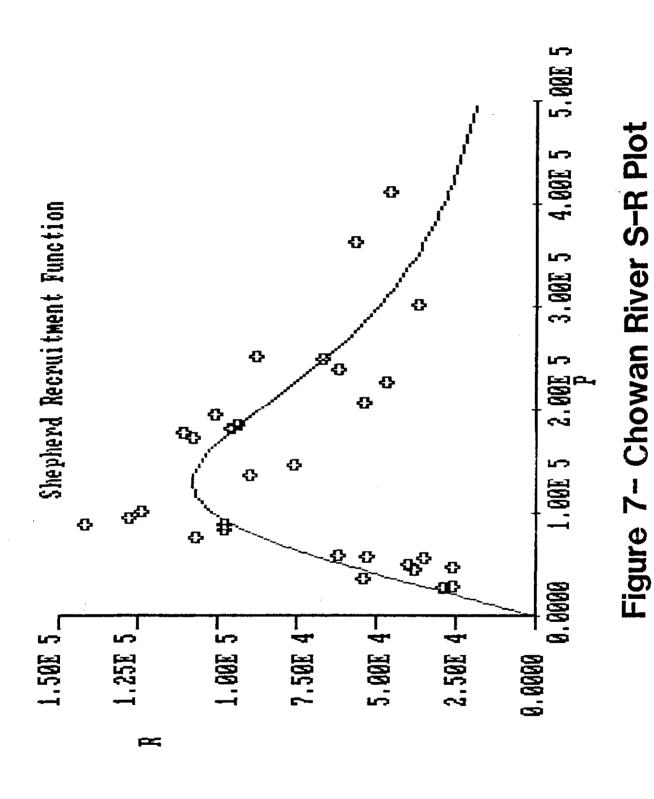


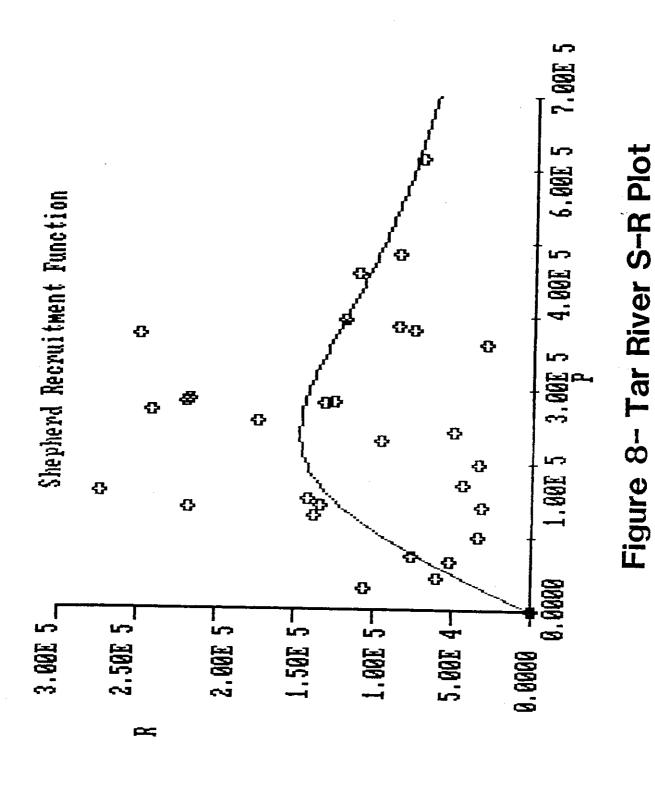
Figure 4- Hudson River S-R Plot

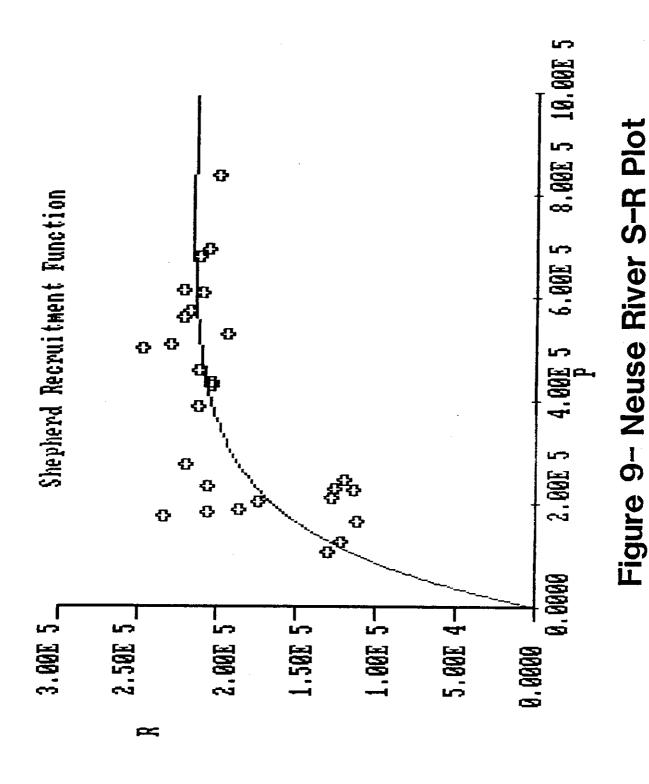


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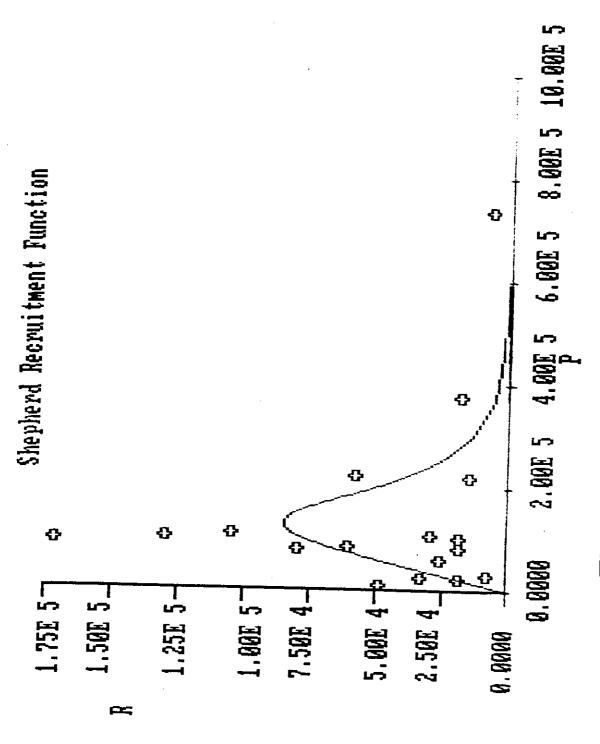


Figure 10- Edisto River S-R Plot

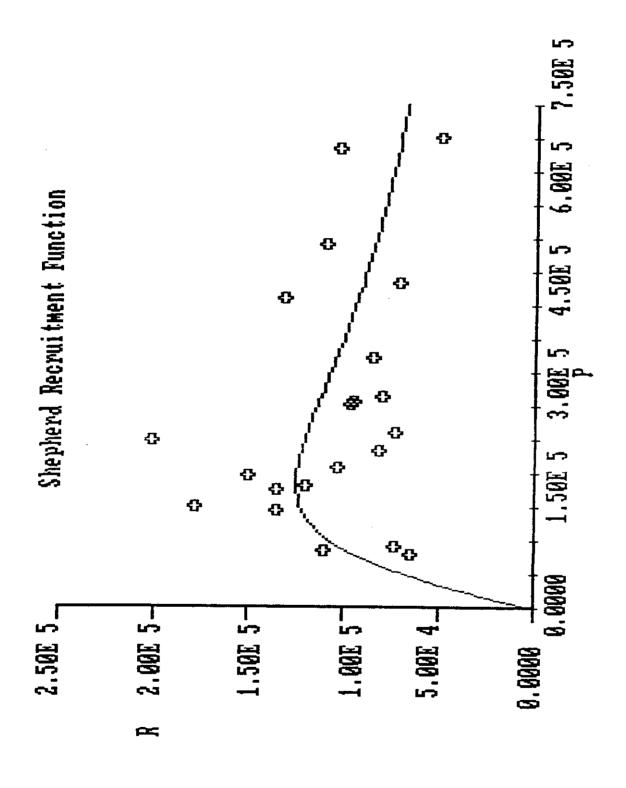


Figure 11- Savannah River S-R Plot

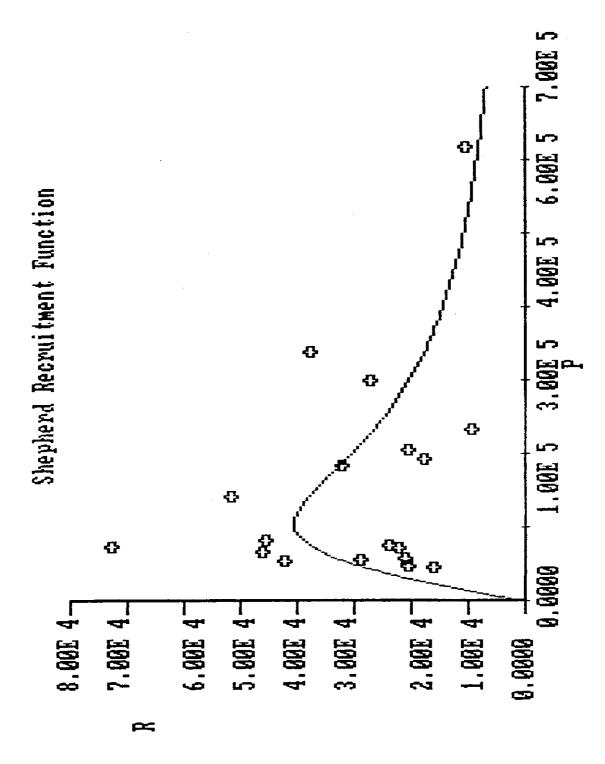
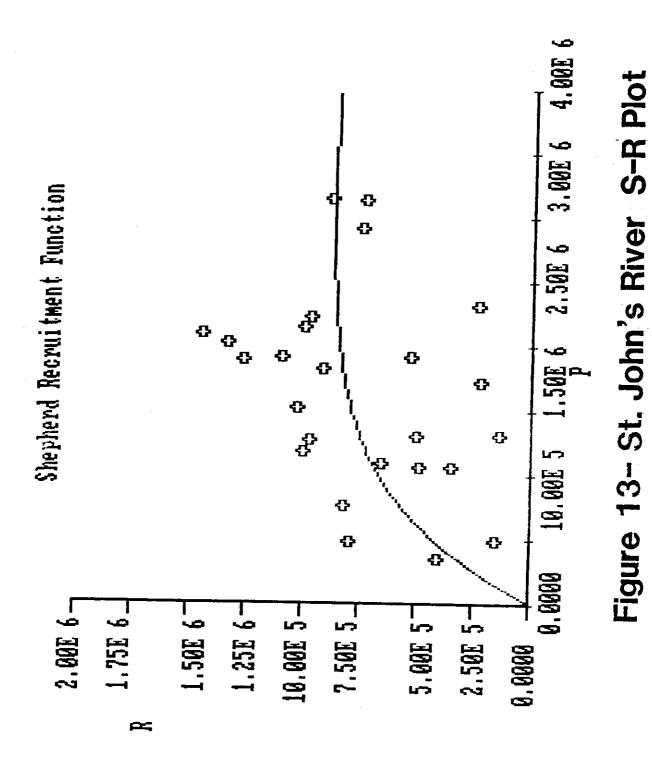


Figure 12- Altamaha River S-R Plot



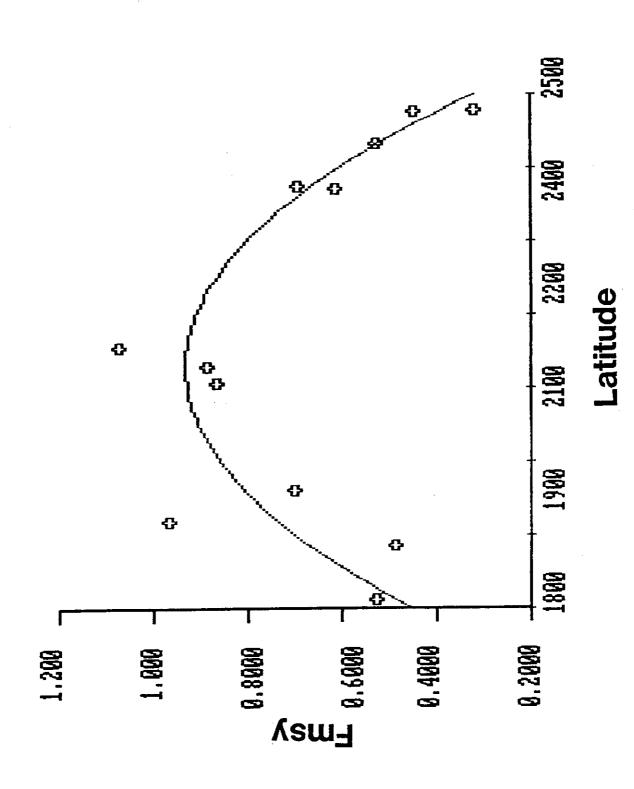
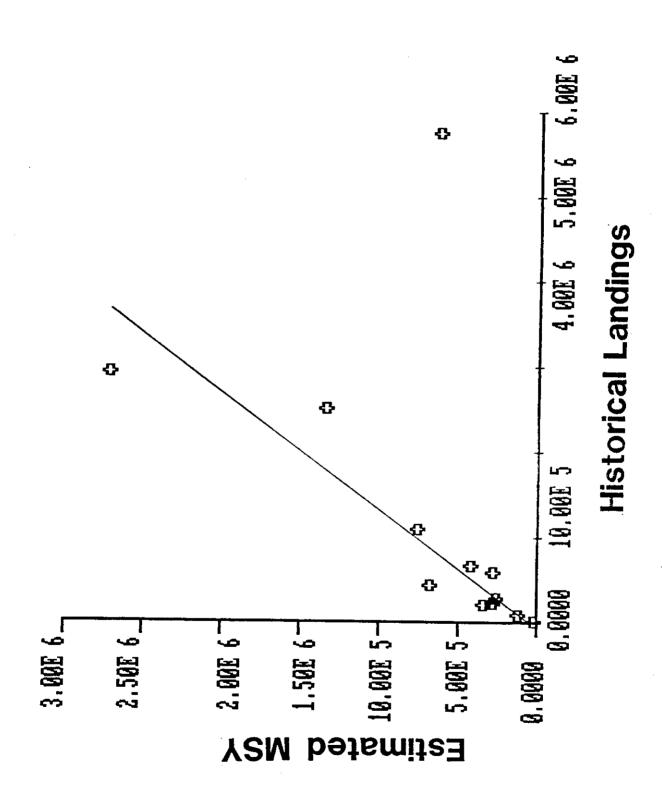


Figure 14- Shad Fishing Rates vs. Latitude



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Figure 16- Shad Fishing Rates vs. Slope of S-R Model

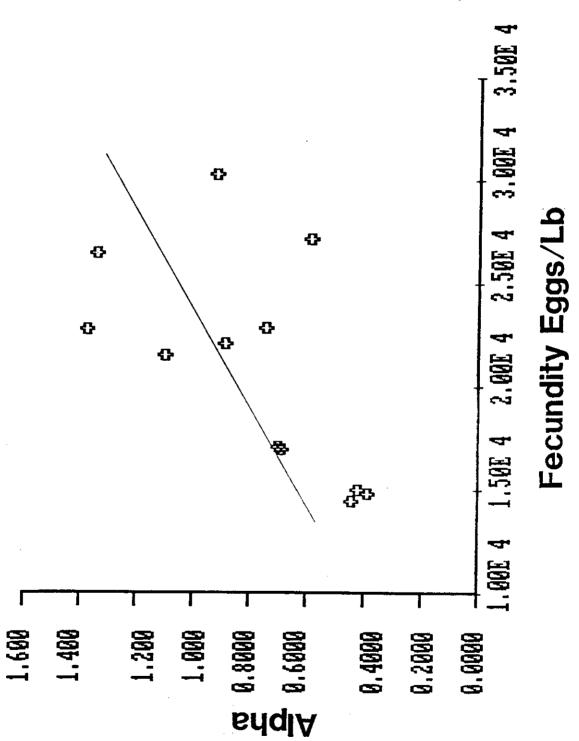


Figure 17- Alpha vs. Fecundity in Shad Rivers

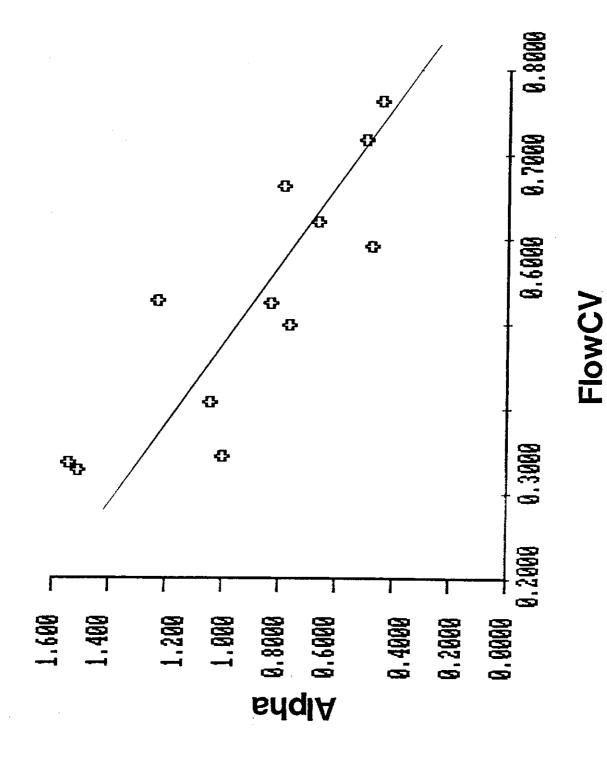
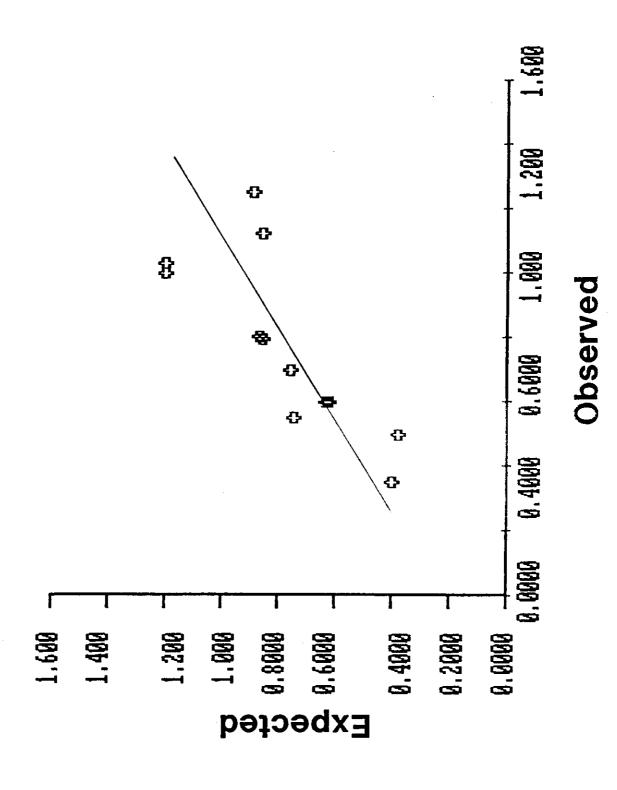


Figure 18- Alpha vs. Flow Variation



APPENDIX 1

American shad recruitment and spawning stock estimates for each river used in the stock-recruitment analysis from north to south

				1/		2/		
	Pawcat R	Pawcatuck River RI.	Connect	Connecticut River CT.	N N	Hudson River NY.	Delaware River NY. NJ. PA.	River J. PA.
Year	Recruitment N x 10	Spawners ₃ lbs x 10	Recruitment N x 10°	Spawners ₃ lbs x 10	Recruitment N x 10	Spawners ₃ lbs x 10 ³	Recruitment N x 10^3	Sp 1b
95	1	٠,	1	1	1280	1308	ı	i
95	ı	1	,		1351	2311	i	í
95	1		i		1185	2604	ı	i
95	1	1	ı	•	1026	2645	ı	ı
95	1	ı	ı	ı	915	3178	1	1
95		ı	ı	1	678	4343	1	1
95	3	1	i	,	1559	5021	1	1
95	1	1	i	1	464	4627	1	1
95	1	1	1	1	324	3248	ι	1
95	1	ı	1	1	240	3938	•	1
96	t	ı	1	i	217	2470	ı	ı
1961	ı	1	ı	1	184	2106	1	ł
96	J	1	ı	ı	238	1916	1	ı
96	1	ı	i	ı	286	1407	ı	1
96	1	1	ì	1	282	785	ì	1
96	,	1	ţ	ı	254	1041	1	1
96		1	257	529	270	555	ı	ŀ
96	B	•	243	768	319	834	ı	•
96	ı	1	200	929	287	1136	ı	1
96	t	•	228	1766	242	1132	,	i
93	1	í	181	1900	213	1041	•	1
97	1	•	290	1950	203	825	ω,	292.2
97	1	į	378	768	303	1377	84.6	118.3
6	1	ı	219	511	462	1168	ė	170.6
9	0	0	273	1408	610	926	0	201.4
97		87	263	1136	681	773	٠	219.0
9	214	786	240	2001	412	754	ı	
9	∞	663	414	952	297	621	t	ſ

APPENDIX 1 continued

ų ·	Spawners lbs x 10									
aware River NY. NJ. PA.	Spaw lbs		181.5	339.7	694.1	105.5	396.8	422.3	707.4	.206.1
Delaware River NY. NJ. PA.	Recruitment N x 10^3	1	84.6				441.3			
2/ Hudson River NY.	Spawners ₃ lbs x 10	2006	1517	3043	ŧ	ſ	,	1	1	1
Hudso	Recruitment N x 10^3	345	396	285	ı	ı	ŧ	•	•	•
1/ Connecticut River CT.	Spawners ₃ lbs x 10 ³	996	1141	1569	1348	2305	ı	ı	ı	i
Connect	Recruitgent Spawners $_{\rm N}$ x $_{10}$ lbs x $_{10}$	449	494	369	302	267	1	1	ŧ	1
Pawcatuck River RI.	Spawners ₃ lbs x 10 ³	513	1146	1416	1198	803	1026	ı	1	1
Pawcat	Recruitment Spawners $_{ m N}$ x 10 $_{ m N}$ lbs x 10 $_{ m S}$	140	312	386	326	219	280		1	1
	Year	1978	1979	1980	1981	1982	1983	1984	1985	1986

1/ Recruitment was Adjusted for June Flow Effects 2/ Hudson River Data Dates Back to 1915

APPENDIX 1 continued

River C. Spawners ₃ 1bs x 10	αουαντα αια αντο αντα αντο ο τα αυτο ο ο ο ο ο ο ο ο ο ο ο ο ο ο ο ο ο ο
· c z	76. 84. 76. 84. 239. 147. 101. 178. 178. 195. 363.
Chowan N. Recruitment N x 10	
mes River Virginia ent Spawners ₃ lbs x 10	1689.0 345.3 219.5
James Virg Recruitment N x 10	732.5 627.7 182.2
e River Delaware Spawners 1bs x 10	258 711 99 126 1126 1118 292 301 408 408 402 292 175 209 243 340
Nanticoke River Maryland, Delawar Recruityent Spawne N x 10	28.0 30.5 27.0 26.8 52.8 51.5 51.5 51.5 31.8 31.8 32.0 55.3 38.0 74.8 74.8 73.0 73.0
a River , PA. Spawners ₃ lbs x 10	2131 923 800 2480 1806 1669 3615 3365 3173 3365 3173 3173 3173 3173 3173 3173 3173 2138 225 580 149 187 213 235
Susquehanna Maryland, Recruitment N x 10	729.4 789.8 1095.5 1312.0 1255.3 1137.5 1037.5 1037.5 1268.0 887.3 805.3 651.3 651.3 651.3 129.8 141.0 100.3 112.5 115.5 80.3 48.6 36.8
Year	1944 1944 1945 1946 1947 1950 1951 1953 1953 1965 1965 1965 1965 1965 1970 1973 1975 1975

APPENDIX 1 continued

River 3.	Spawners, lbs x 10	136.6	88.8	24.2	58.1	76.3	193.7	282.3	ı
Chowan River	Recruitgent Spawners, N x 10 lbs x 10		6.86	1	1	ı	-	- 2	i
James River Virginia		246.6	123.0	9.89	12.5	146.8	174.7	472.1	22.0
	Recruitment Spawners $_3$ N x $_10$ lbs x $_10$	576.2	241.0	334.7	92.7	36.7	117.4	139.5	55,5
Nanticoke River Maryland, Delaware	Spawners ₃ lbs x 10 ³	·	1	1	1	i	1	ı	ı
Nanti Maryla	Recruityent Spawners ₃ N x 10 lbs x 10	ι	ì	t	ı	1	1		1
nna River nd, PA.	Spawners ₃ lbs x 10	ı	ı	i	1	1 .	•	•	ŧ
Susquehanna River Maryland, PA.	Year Recruitment N x 10:			ı	t	ŧ	1	1	1
	Year	1978	1979	1980	1981	1982	1983	1984	1985

	Neuse	River	Tar-Pamlico	co River C.	E E	ar River C.	Pee De	Dee River S.C.
Year		Spawners ₃ lbs x 10 ³	Recruitment N x 10	Spawners lbs x 10	Recruitment N x 10	Spawners ₃ lbs x 10	Recruitment N x 10°	ı li
6	ι	1	138.7	128.2	16.2		. 1	1
O,	1	1	35	4	16.6	2	1	ı
9	30.	07.	-	O.	•	75.1	17.0	ъ
0	22.	26.	α	387.1	10.2		20.3	0
1954	113.3	166.8	77.3	381.8	6.9	9.69	25.7	3.05
σ	15.	25.	97.9	Ó	12.1		•	
9	26.	28.	\sim	83			29.9	
Q	21.	45.	$^{\circ}$	80	20.6	6	•	۲.
Ο,	29.	11.	4	51	6	25.9	•	
Q,	74	03.	\vdash	3	7		31.7	0.
O	.90	84.	75	5	23.6		•	4.
Ò	20.	76.	18	87		47.2	18.0	ω.
σ	07.	32.	20	83.	8	2		4.
g,	35	77.	٠. دا	~		56.9		٥.
Ċυ.	48.	00.	50.	74.	Ď,	6	16.9	'n
Φ.	94.	29.	25.	96.	7	σ		_
Q,	18.	72.	74.	56.	7	ж ж	21.4	Ġ
ġ.	05	28.	12.	59.	2	ö		m
ġ.	13.	57.	86.4	84.	4	੍ਹਾਂ ਹਾ	•	ij
S.	00	36.	73.4	14.	4	91.9	45.9	30.
g	86.	87.	51.0	43.	•	02.	٠,	38.
σ	07.	93.	31.3	61.		ġ.	•	Ċ
O	05.	37.	34.4	199.3	13.5	54	٠	28.
O)	10.	08.	45.7	70.	•	66.4	•	64.
σ.	22	62.	33.5	ij.	7	ä	•	
י תם	12.	88	34.8	0	Ġ.	ω.	•	99
יים	12.	77.	52.4	7.	_•	12.2	-	-
יים	23.	13.	61.6	44.0	ä	7	•	2
ου ∘	30.	08.	9.92	75.3	ġ.	43.9		8.01
Ġ,	1	94.	106.3	0	1	8	•	27.4
ο		71.	i	30.3	1	6	•	g
σ.	ı	84.	ı	급	1	17.6	•	22.7
σ,	t	36.		ė.	1	٠	•	57.8
٥		82.	1	98.5	ì			ø
ĊΟ.	•	76.	1	6	1	11.1		7
φ.	i	1	1	1	1			137.6
σ,		i	ι	ı	ı	ı	33.9	

Altamaha River Georgia tment Spawners	1bs x 10 ³	82.9	55.0	67.7	75.4	143.4	339.7	301.6	194.3	617.7	233.4	J	,	•	48.7	47.1	72.9	76.5	59.4	185.3	56.9	205.5	•	ı	1	•	•	1
Altamal Geo	N × 10 ³	45.7	42.5	46.6	73.2	52.2	37.9	27.7	18.3	10.9	9.8	•	ı	4	20.8	16.4	22.6	24.1	21.2	32.6	29.0	20.7	•	1	ŧ	1	•	-
h River gia Spampers	1bs x 10 ³	ı	1	r	79.8	91.0	175.6	249.1	151.3	181.1	144.4	302.5	682.8	701.2	260.2	541.8	197.8	461.1	85.4	208.8	233.9	483.3	372.9	315.0	307.0	ı	1	ţ
Savannah River Georgia Roccuitment	$N \times 10^3$	ł	1	1	66.3	74.8	136.4	201.8	179.8	121.6	135.9	~2.96	104.2	51.0	73.9	110.4	150.2	132.4	110.9	104.5	82.7	72.2	85.3	80.5	96.5	ı	ı	1
iver	1bs x 10 ³	109.5		86.0	112.0	97.0	102.7	81.4	224.5	377.0	735.4	410.4	215.2	231.3	10.8	26.1	30.3	•	23.8	221.3	102.6	61.8	82.8	64.1	42.2	64.6	110.6	65.5
Edisto River N.C.	N x 10 ³	29.8	•	61.1	105.2	172.0	130.8	79.8	59.1	19.1	8.9	ı	r	1	49.5	33.6	8.8	22.3	19.1	15.7	19.9	27.3	19.8	•	ı		ŧ	1
	Year	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986

			And the second s																									
Ver	Μner	lbs.x10 ³	661122	978363	832974	802782	1007829	972245	924419	1035505	1450362	1340246	1106188	1277365	894501	745316	1001394	753117	528518	510522	241745	235127	360612	142842	155386	410743	497156	
St. John's River	=	$N \times 10^3$	95	277	<u> </u>	84	187	220;	828(525;	9860	0268	9158	894(141;	1363	2144468	9149	914(3088	3111	7275	3690	3153	328	312	S.	
		Year	1950	<u></u>	õ	ŏ	8	5	<u>~</u>	3	χ.	2	χ.	196	8	8	9	9	9	8	9	9	\simeq	\simeq	$\tilde{\sim}$	$\stackrel{\sim}{\sim}$	\sim	

