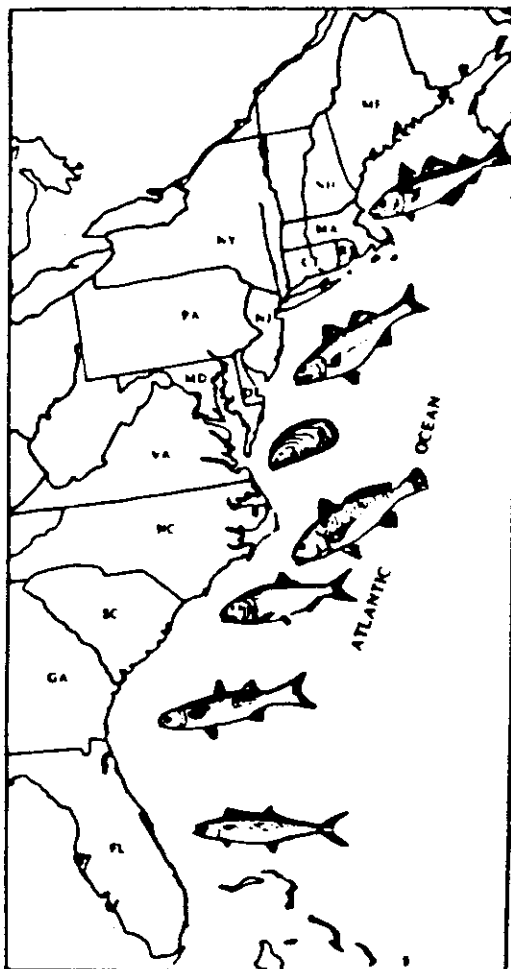


Special Report No. 15
of the

ATLANTIC STATES MARINE FISHERIES COMMISSION



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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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 ($r^2=0.64$), Delaware River ($r^2=0.521$), Neuse River, North Carolina ($r^2=0.436$), whereas the worst fits occurred for the Tar River, North Carolina ($r^2=0.110$), St. Johns River, Florida ($r^2=0.144$), Savannah ($r^2=0.223$) and Altamaha ($r^2=0.224$) 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 (F_{msy}) 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 F_{msy} level. The current fishing rates for the other shad rivers were well below F_{msy} 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 F_{msy} 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 F_{msy} estimates, however, are subject to several sources of bias including measurement errors in the catch-effort and stock-recruitment data, poor precision about the F_{msy} 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 (F_{msy}) 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 F_{msy} 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 (F_{msy}) 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 F_{msy} level, and 3) examine to what extent latitudinal variability in MSY and F_{msy} 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 (r^2) 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):

$$Erel = Ct/CPUE \quad (1)$$

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:

$$N_t = C_t / (1 - \exp(-q \cdot E_t)) \quad , \quad (2)$$

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):

$$q = R_t / (M_t \cdot E_t) \quad . \quad (3)$$

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 (F_t) for each year by the corresponding fishing effort (E_t):

$$q = F_t/E_t \quad (4)$$

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

$$C_t = q \cdot E_t \cdot B - (q^2 \cdot B/K) \cdot E_t^2. \quad (5)$$

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 (P_t) in each year was the annual population estimate (N_t) 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 (N_t), 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 (R_t) 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 (R_t) and spawning stock (P_t) for

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

$$R_t = a * P_t / [1 + (P_t / K)^B], \quad (6)$$

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 ($CV = SE / \text{mean}$). 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 F_{MSY} 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:

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

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

$$R = P / (B/R) \quad (8)$$

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

$$Y = R * Y/R. \quad (9)$$

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:

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

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

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

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 than 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:

$$Fmsy = b_0 + b_1(X_1) + b_2(X_2) + b_3(X_3) \quad (12)$$

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 (X_i) 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 (X_i), we used jackknife and cross-validation methods (Miller 1974; Efron 1982) to estimate the magnitude and direction of bias in predicting F_{msy} for each river. The jackknife method involves predicting F_{msy} with equation (12) for each river without including the predictor variables (X_i) 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 (b_0, b_1, b_2, b_3) and their standard errors (SE). To complete the cross-validation procedure, the F_{msy} values from the Shepherd model (equation 6) were linearly regressed against the jackknife estimates of F_{msy} (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 F_{msy} with high precision for the 12 American shad stocks, realistic estimates of F_{msy} 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 (F_{msy}) for those rivers by substituting their respective life history and abiotic factors (X_i) into equation (12).

Results

Stock-Recruitment Properties of Each Stock-The degree of fit (r^2) 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 r^2 criterion of 0.10 (range: 0.11-0.62). There was no apparent latitudinal pattern in the magnitude of the r^2 values among the 12 stocks. The Shepherd S-R model best described the stock-recruitment data in the Chowan ($r^2=0.624$), Delaware ($r^2=0.521$) and Neuse ($r^2=0.436$) rivers, whereas the worst fits occurred in the Tar ($r^2=0.11$), St. Johns ($r^2=0.144$), Savannah ($r^2=0.223$) and Altamaha ($r^2=0.224$) 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.

Factors 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 exhibit 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 F_{msy} are highly sensitive to the slope parameter (α) in the S-R model. The significant correlations between the (α) parameters and fecundity and between (α) 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 (α) estimates is consistent with this hypothesis. The significant inverse relationship between the (α) 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 F_{msy} 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 F_{msy} levels. Moreover, because of short-term changes in recruitment due to variability in environmental factors, the MSY and F_{msy} values given in this study should be considered long-term averages. No attempt has been made to estimate confidence limits on our estimates of F_{msy} 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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Literature Cited

ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery Management Plan for the Anadromous Alosid Stocks of the Eastern United States: American Shad, Hickory shad, Alewife, and Blueback Herring: Phase II in Interstate Planning for Alosid of the Atlantic Coast. Washington, D.C.

Chittenden, M.E. 1969. Life history and ecology of the American shad, Alosa sapidissima, in the Delaware River. Ph.D. Dissertation. Rutgers Univ., New Brunswick, NJ. 459p.

Crecco, V.A., and M.R. Gibson. 1987. Methods of estimating fishing mortality rates on American shad. Report to the Atlantic States Marine Fisheries Commission. 14p.

Crecco, V.A., and T.F. Savoy. 1985. Density-dependent catchability and its potential causes and effects on Connecticut River American shad, (Alosa sapidissima). Can. J. Fish. Aquat. Sci. 42:1649-1657.

Crecco, V.A., and T.F. Savoy. 1987. Review of recruitment mechanisms of the American shad: (Alosa sapidissima) in critical periods and mis-match hypotheses re-examined. American Fisheries Society Symposium 1:455-468.

Crochet, D.W., D.E. Allen, and M.L. Hornberger. 1976. Evaluation of commercial fisheries for American shad in South Carolina and status of the species in selected waters. pp 1-17. In: Proceedings of a Workshop on American Shad. U.S. National Marine Fisheries Service. 14-16 Dec. 1976. Amherst MA.

Cushing, D.H., and J.G.K. Harris. 1973. Stock and recruitment and the problem of density dependence. *Rapports et Process-Verbaux des Reunions Conseil International pour l'Exploration de la Mer* 164:142-155.

Cushing, D.H. 1981. *Fisheries Biology: a Study in Population Dynamics*, 2nd. Edition. Univ. Wisconsin Press.

Davis, W.S. 1957. Ova production of American shad in Atlantic coast rivers. U.S. Fish and Wildlife Service Res. Rep. No. 49.

Draper, N.R., and H. Smith. 1981. *Applied Regression Analysis*, 2nd. Edition. John Wiley and Sons. New York, NY. 709p.

Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. *Society for Industrial and Applied Mathematics, Regional Conference Series in Applied Mathematics, Monograph 38*, Philadelphia, PA.

Fredin, R.A. 1954. Causes of fluctuations in abundance of Connecticut River shad. U.S. Fish and Wildlife Service Fishery Bulletin 54:247-259.

Garrod, D.J. 1982. Stock and recruitment- again. Great Britain Ministry of Agriculture Fisheries and Food Directorate of Fisheries Research. Fisheries Technical Report 68.

Garrod, D.J., and J.W. Horwood. 1984. Reproductive strategies and the response to exploitation. Chapter 20, G.W. Potts and R.J. Wootton, eds., Fish Reproduction: Strategies and Tactics. Academic Press, London, 410p.

Gibson, M.R., and J.F. O'Brien. 1988. Shad Restoration Studies. Performance Report. Rhode Island Division Fish and Wildlife. Job Number F-26-R-III-3. 38p.

Hankin, D.G., and M.C. Healey. 1986. Dependence of exploitation rates for maximum yield and stock collapse on age and sex structure of chinook salmon (Oncorynchus tshawytscha) stocks. Can. J. Fish. Aquat. Sci. 43:2746-1759.

Hoenig, J. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82(1):898-903.

Jensen, A.L. 1986. Assessment of the Maine lobster fishery

with surplus production models. N. American J. Fish. Mgt.
6:63-68.

Klauda, R.J., M. Nittel, and K.P. Campbell. 1976.
Commercial fishery for shad in the Hudson River: fish
abundance and stock trends, pp. 107-134. In: Proceedings of
a Workshop on American shad. U.S. National Marine Fisheries
Service. 14-16 Dec. 1976. Amherst MA.

Koo, Ted. S.Y. 1970. The striped bass fishery in the
Atlantic States. Chesapeake Science. Vol.II. No.2:73-93.

Leggett, W.C. 1969. Studies on the reproductive biology of
the American shad (Alosa sapidissima). A comparison of
populations from four rivers of the Atlantic seaboard.
Ph.D. Dissertation. McGill Univ. 125p.

Leggett, W.C. 1976. The American shad, Alosa sapidissima,
with special reference to its migrations and population
dynamics in the Connecticut River, pp. 168-225. In: D.
Merriman and L.M. Thorpe, eds., The Connecticut River
Ecological Study: the Impact of a Nuclear Power Plant.
Amer. Fish. Soc. Monogr. I. 252p.

Leggett, W.C., and J.E. Carscadden. 1978. Latitudinal
variation in reproductive characteristics of American shad
(Alosa sapidissima): evidence for population specific life
history strategies in fish. J. Fish. Res. Board Can.
35:1469-1478.

Lehman, B.A. 1953. Fecundity of Hudson River shad. U.S. Fish and Wildlife Service Res. Rep. No. 33.

Lettenmaier, D.P., and J.E. Richey. 1979. Theoretical systems ecology, Chapter 3, In: E. Halfon, ed., Academic Press, New York, NY. pp. 90-104.

Lorda, E., and V.A. Crecco. 1987. Stock-recruitment relationship and compensatory mortality of American shad in the Connecticut River. In: M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper, eds., American Fisheries Society Symposium 1:469-482.

Lupine, A.J. 1986. Summary of activities related to American shad and river herring. New Jersey Division of Fish, Game, and Wildlife.

Marcy, B.C. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee plant. In: D. Merriman and L.M. Thorpe, eds., The Connecticut River Ecological Study: the Impact of a Nuclear Power Plant. American Fisheries Society Monogr. 1 252p.

Michaels, R. 1984. Population dynamics of the American shad in the Altamaha River. Interim Rep. 1982-1987. Project No. G-3. Georgia Dept. Nat. Res., Game and Fish Div., Atlanta, GA. 39p.

Miller, R.G., Jr. 1974. The jackknife: a review. *Biometrika* 61:1-15.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Explor. Mer.* 39:175-192.

SAS (Statistical Analysis Systems). 1985. SAS users guide: statistics. SAS Institute, Cary, NC.

Shepherd, J.G. 1982. A versatile new stock-recruitment relationship, and the construction of sustainable yield curves. *J. Cons. Explor. Mer.* 40:67-75.

Sissenwine, M.P., and J.G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* 44:913-918.

Summers, K.J., and K.A. Rose. 1987. The role of interactions among environmental conditions in controlling historical fisheries variability. *Estuaries* 10(3):255-266.

Sykes, J.E. 1956. Shad fishery of the Ogeechee River, Georgia, 1954. U.S. Fish and Wildlife Service, Spec. Sci. Rept. Fish. 191: 11p.

Sykes, J.E., and B.A. Lehman. 1957. Past and present Delaware River shad fishery and consideration for its future. U.S. Fish and Wildlife Service Res. Rep. No. 46.

Talbot, G.E. 1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish and Wildlife Service Fish. Bull. 56:373-413.

Thompson, W.F., and F.H. Bell. 1934. Biological statistics of the Pacific halibut fishery. 2. Effects of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. (Pacific halibut) Comm. No. 8. 49p.

Tukey, J.W. 1977. Exploratory data analysis. Addison-Wesley, Reading, MA.

Walburg, C.H. 1960. Abundance and life history of shad, St. Johns River, Florida. U.S. Fish and Wildlife Service Fish. Bull. 60:487-501.

Walburg, C.H., and R.P. Nichols. 1967. Biology and management of the American shad and status of the fisheries. Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service Special Sci. Rep. Fish. No. 550.

Walters, C.J. 1985. Bias in the estimation of functional relationships from time series data. Can. J. Fish. Aquat. Sci. 42:147-149.

Walters, C.J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Can. J. Fish. Aquat. Sci. 38:701-710.

Welch, D.W. 1987. Frequency domain filtering of age-structured population data. Can. J. Fish. Aquat. Sci. 44:605-618.

Winters, G.H., and J.P. Wheeler. 1987. Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 44:882-900.

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 Commercial Fishery
Connecticut River Connecticut Massachusetts	1.8×10^{-4}	Based on 1966-73 and 1977-80 tag-recapture studies (Leggett 1976; Minta 1980)
Hudson River New York	3.5×10^{-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 studies (Lupine 1986)
Susquehanna River Maryland Pennsylvania	1.8×10^{-6}	Based on 1951 tag-recapture study (Walburg 1955)
Nanticoke River Delaware	8.3×10^{-6}	Estimated indirectly using fishing effort in Nanticoke River in 1951 plus the mark-capture F estimates in Chesapeake Bay (Walburg 1955)

Table 1 continued

James River Virginia	2.0×10^{-5}	Based on 1954 tag-recapture study (Walburg and Skyes 1957) and 1977-80 catch curve analysis (Bruce Hill pers comm) with natural mortality (M) = 1.4 by Hoenig (1983) method
Chowan River North Carolina	1.1×10^{-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-recapture 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-recaptures, Sykes 1956
St. John's River Florida	3.5×10^{-4}	Based on 1953-1958 tag-recaptures, Walburg 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			
	a	B	K	r^2
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.

River	S-R Parameters			Geometric Mean CV
	a	B	K	
	Coefficient 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 (U_{msy}), F_{hist} , and historical yields for 12 shad rivers.

River	F_{msy}	U_{msy}	MSY(lbs)	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 F_{msy} for 12 Atlantic shad rivers, as well as parameter estimates and their standard errors.

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

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>	<u>P/b = 0</u>
b_0	-18.2630	-	-	-
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_{msy} for 12 Atlantic coast shad stocks

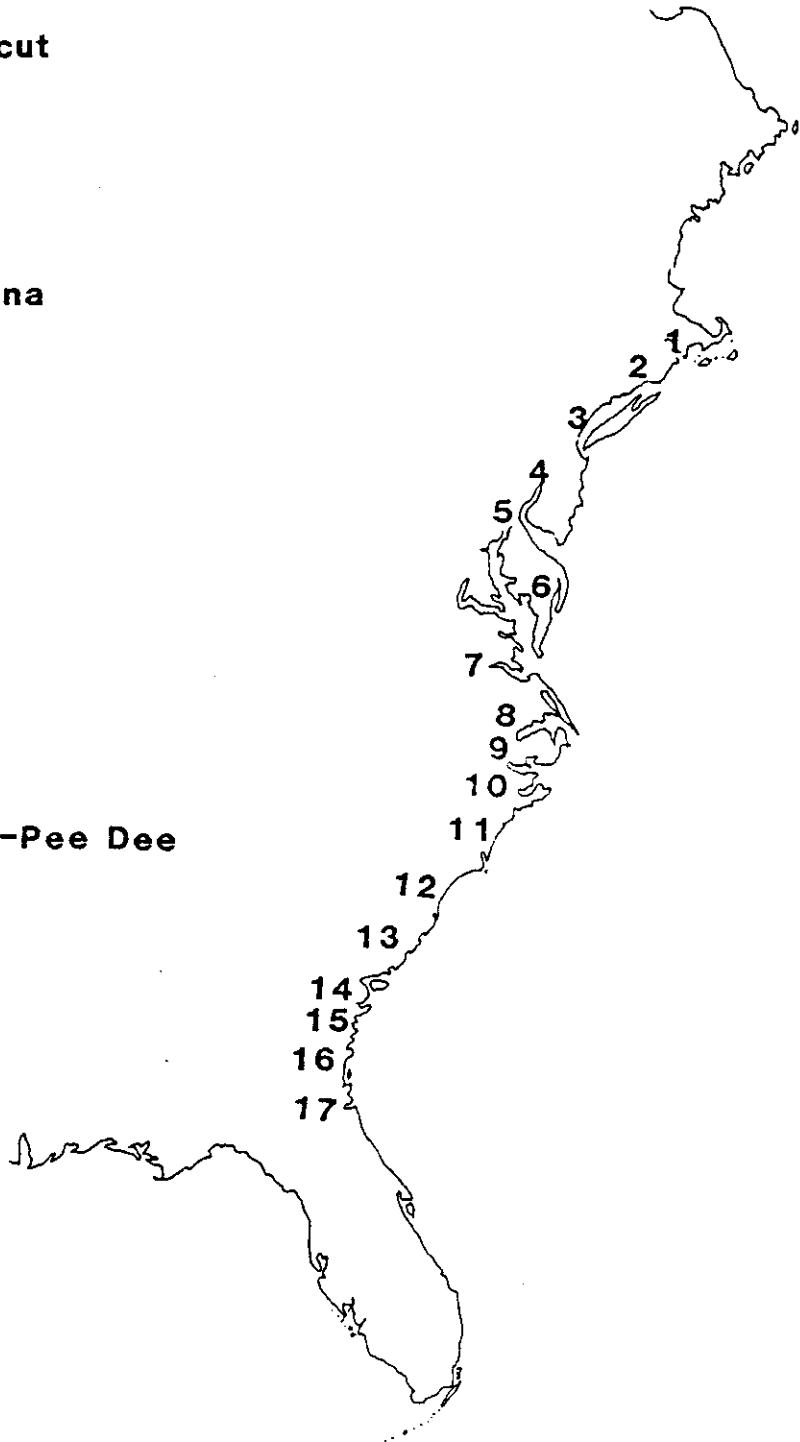
River	Assessed F_{msy}	Predicted F_{msy}	Deviation	SE Reg.	95% CI
Pawcatuck	0.350	0.409	-0.059	0.144	0.121 - 0.697
Connecticut	0.500	0.385	0.115	0.141	0.103 - 0.667
Hudson	0.600	0.636	-0.036	0.145	0.346 - 0.926
Delaware	0.795	0.857	-0.062	0.145	0.567 - 1.147
Susquehanna	0.700	0.765	-0.065	0.145	0.475 - 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 (F_{msy} , U_{msy}) for several other shad rivers along the Atlantic Coast from the multiple regression model

River	F_{msy}	U_{msy}	95% CI on F_{msy}	F_{curr}
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 Dee	1.260	0.716	0.998 - 1.532	0.690
Ogeechee	1.062	0.654	0.790 - 1.335	0.966

Figure 1- EAST COAST SHAD RIVERS Examined in Stock Assessment

- 1 Pawcatuck
- 2 Connecticut
- 3 Hudson
- 4 Delaware
- 5 Susquehanna
- 6 Nanticoke
- 7 James
- 8 Chowan
- 9 Tar
- 10 Neuse
- 11 Cape Fear
- 12 Waccamaw-Pee Dee
- 13 Edisto
- 14 Savannah
- 15 Ogeechee
- 16 Altamaha
- 17 St. John



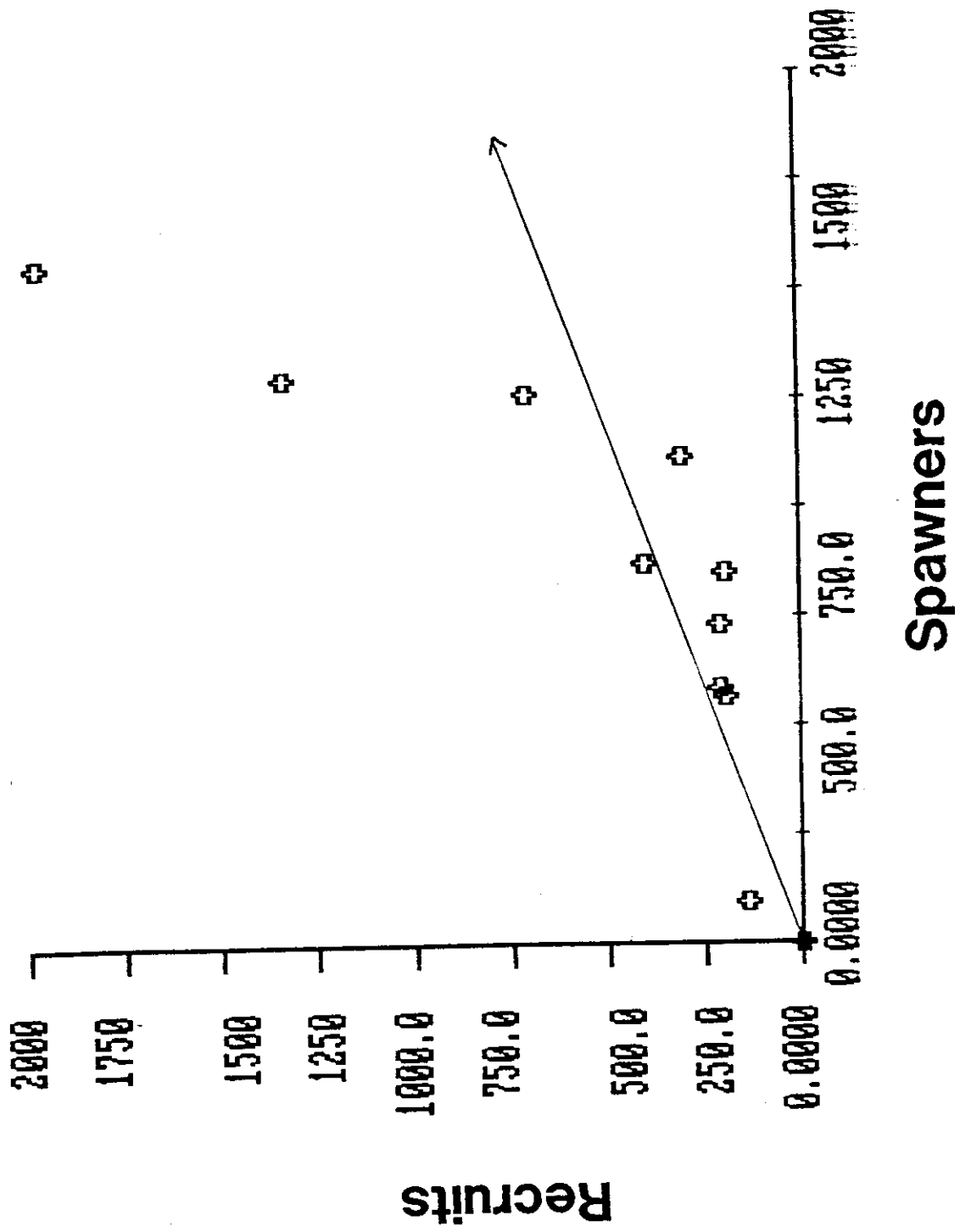


Figure 2 Pawcatuck River S-R Plot

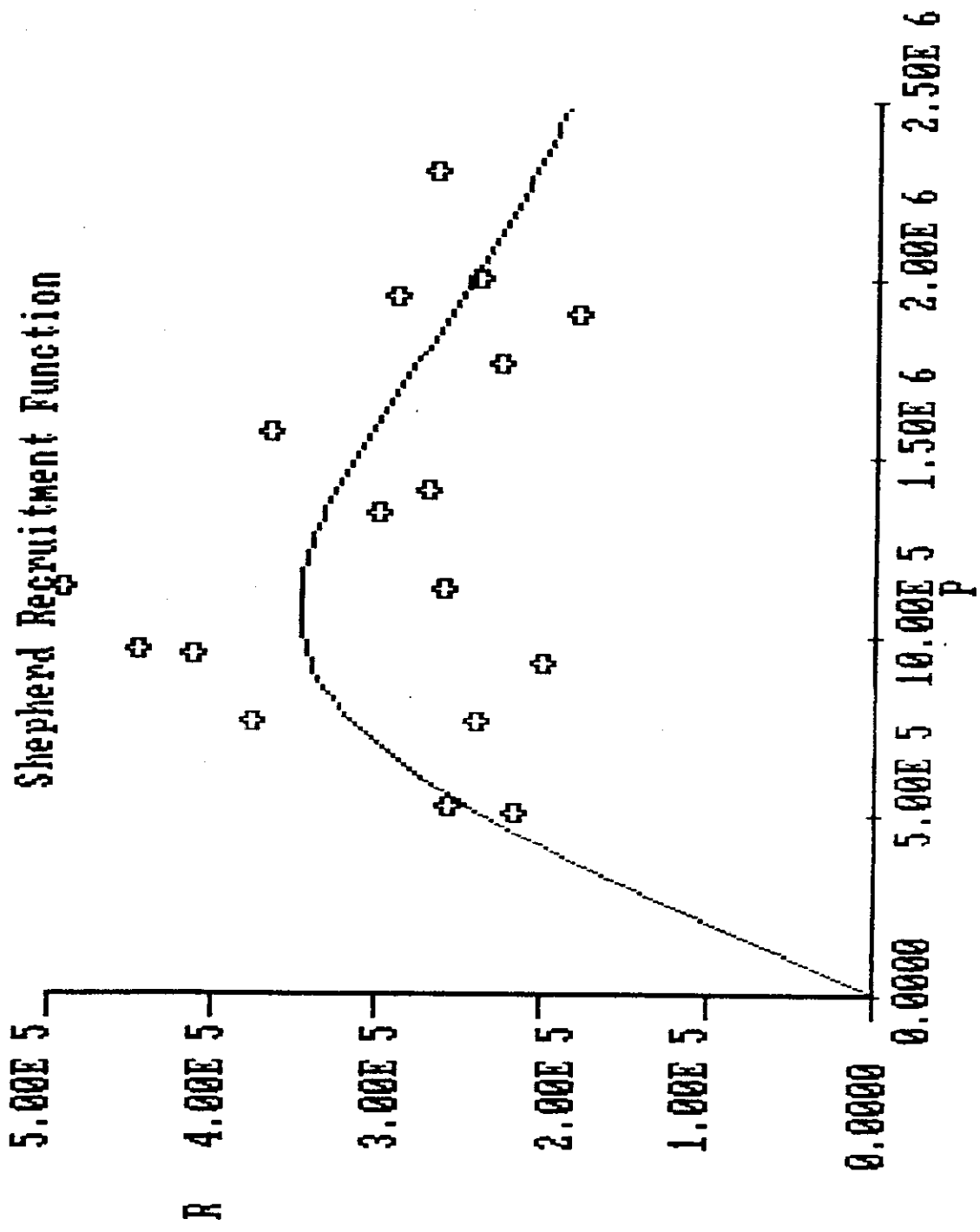


Figure 3- Connecticut River S-R Plot

Shepherd Recruitment Function

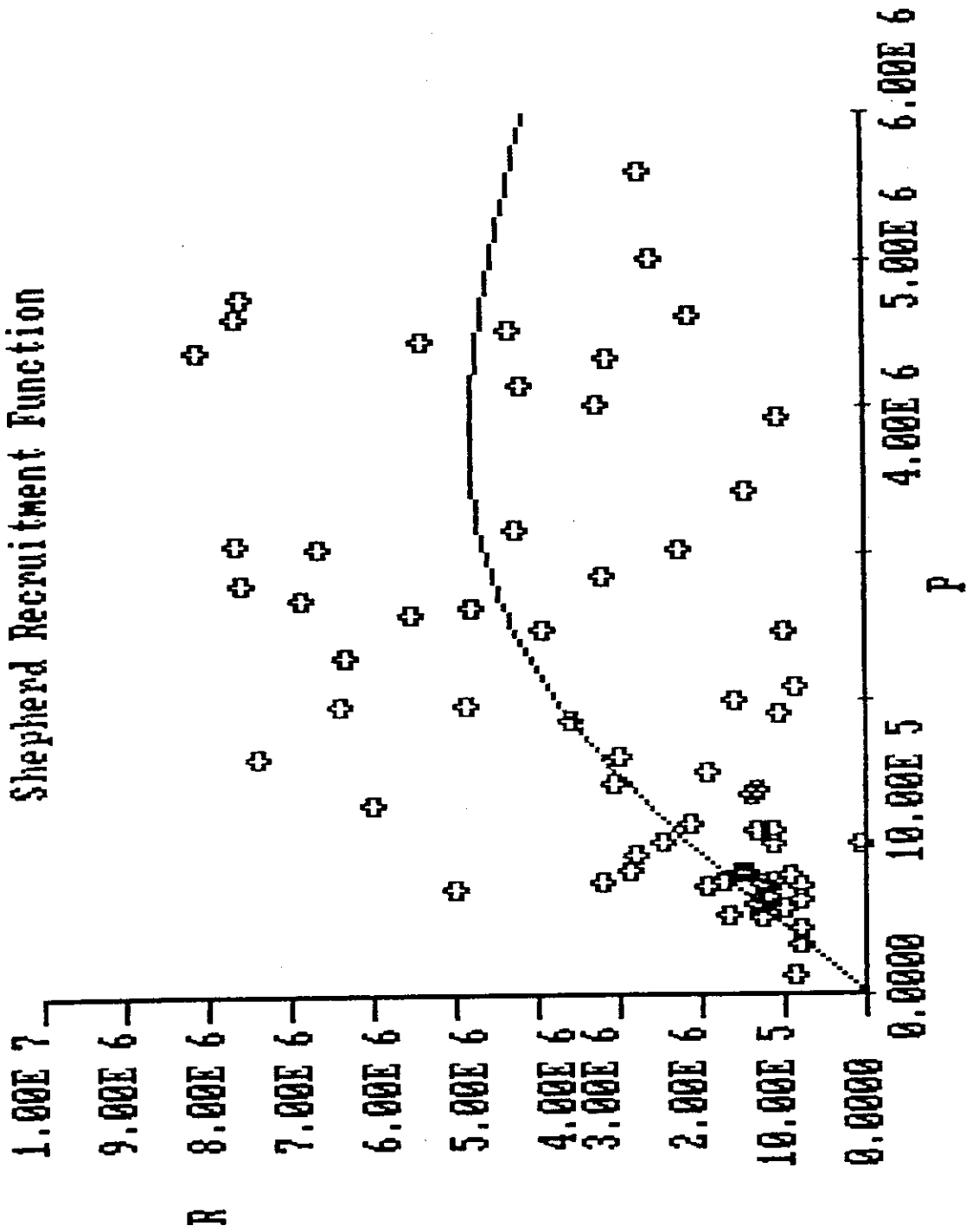


Figure 4- Hudson River S-R Plot

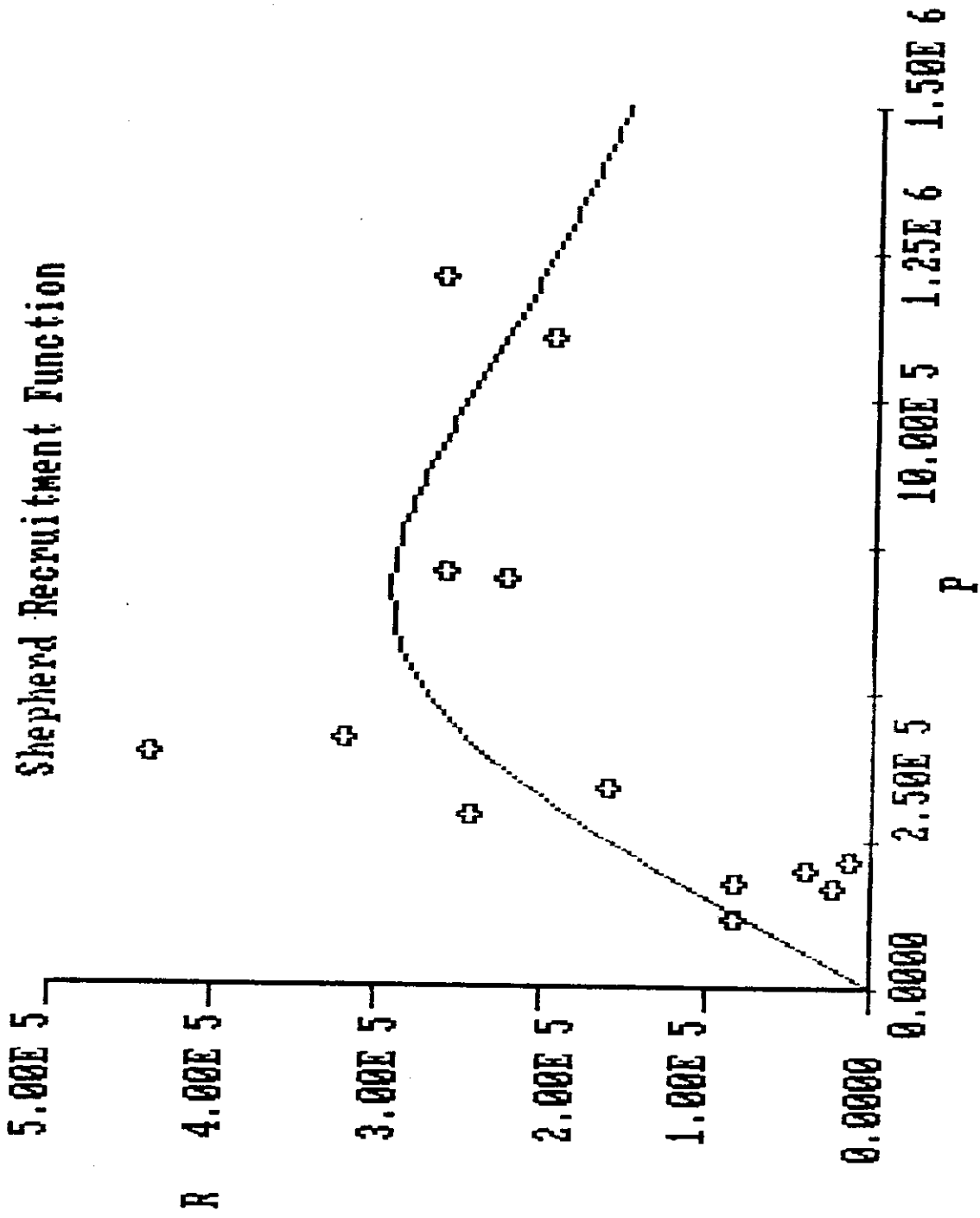


Figure 5- Delaware River S-R Plot

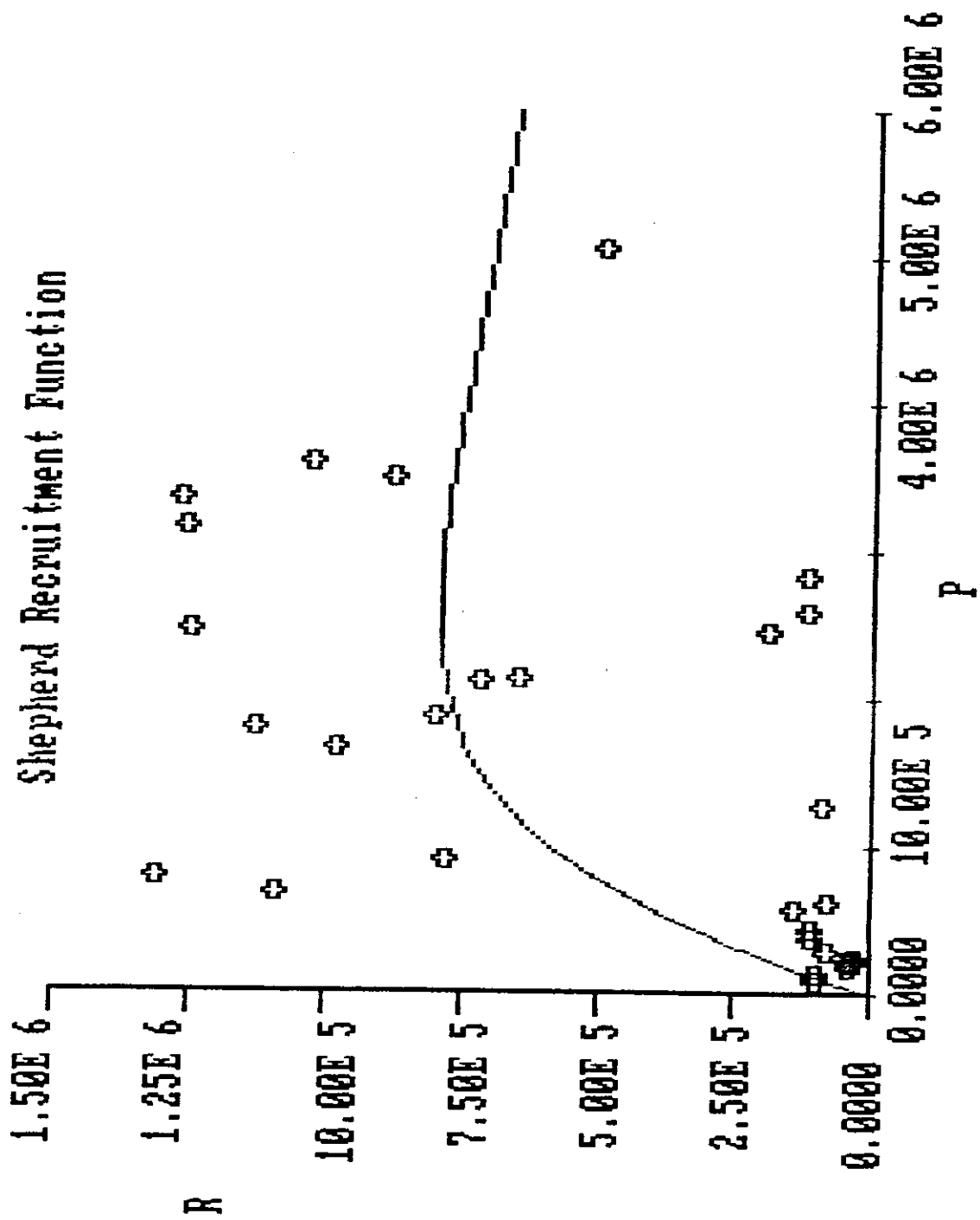


Figure 6- Susquehanna River S-R Plot

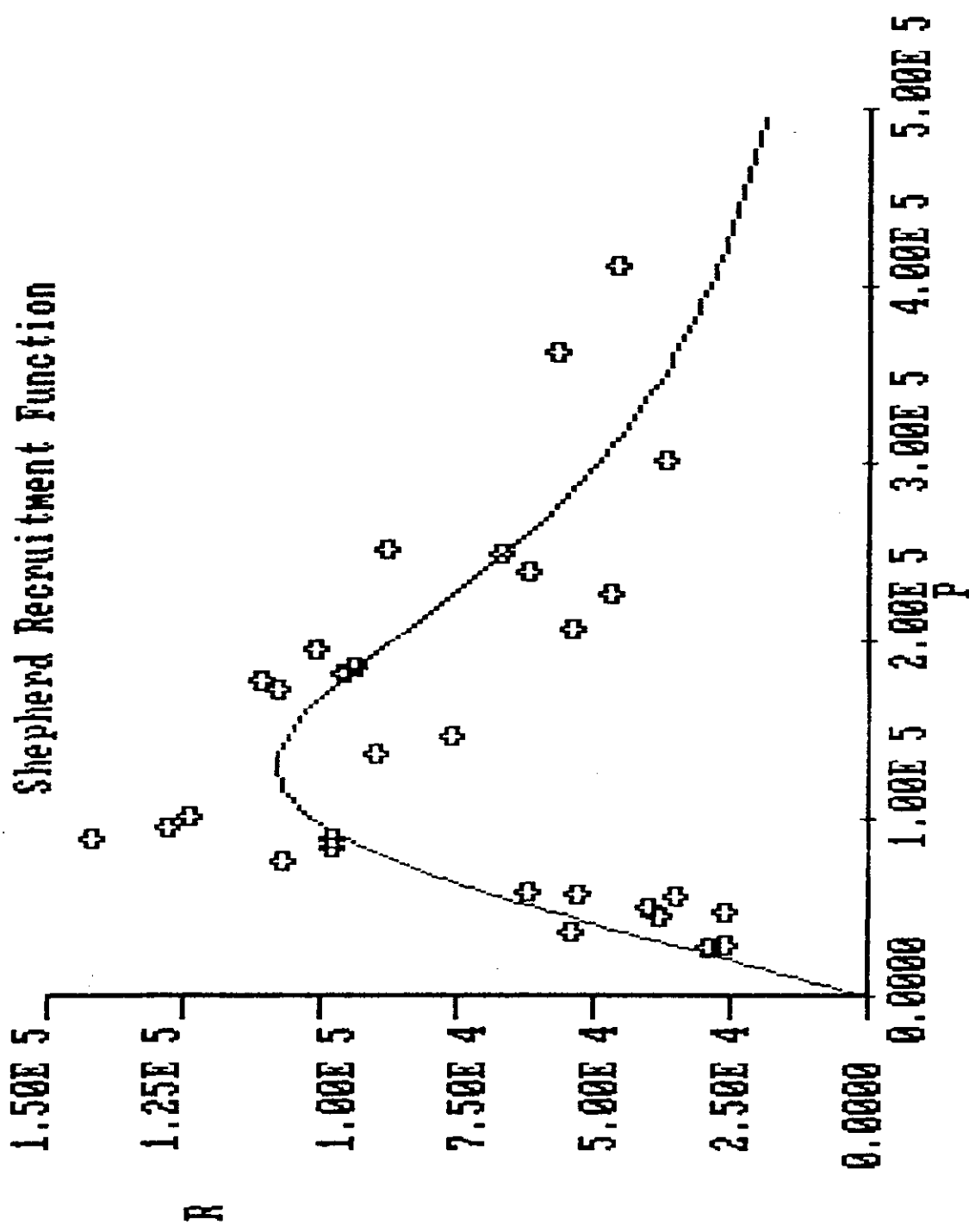


Figure 7-- Chowan River S-R Plot

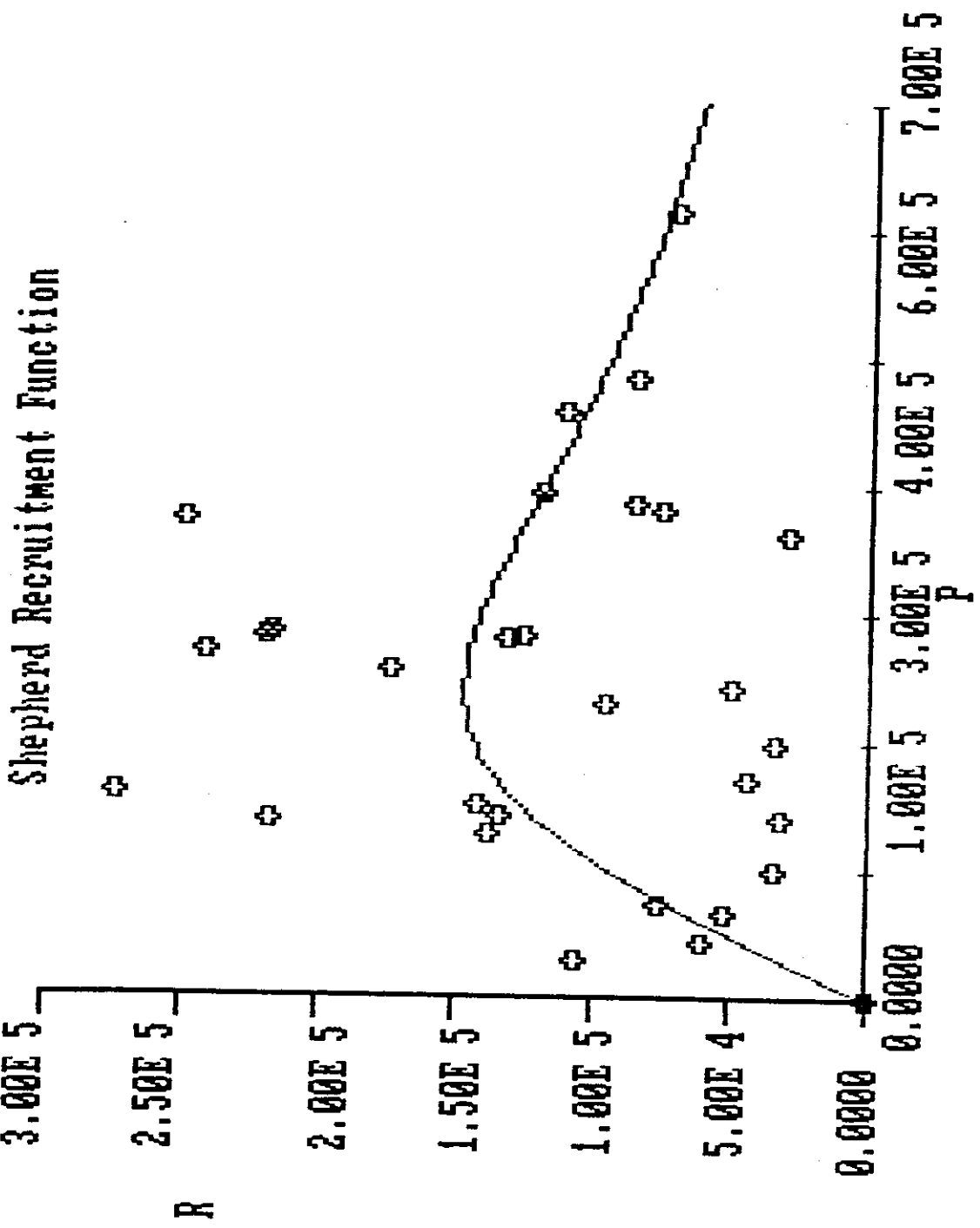


Figure 8- Tar River S-R Plot

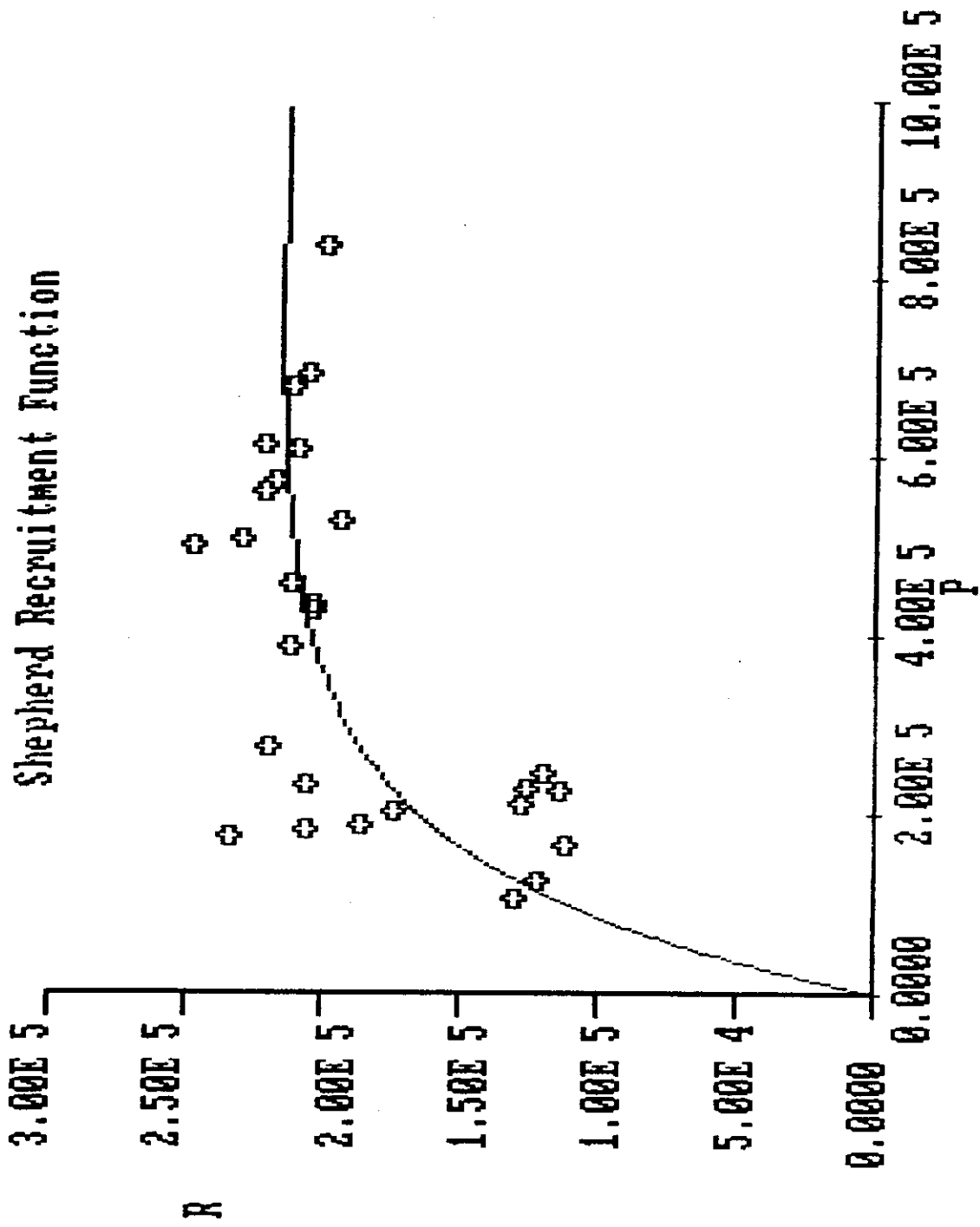


Figure 9- Neuse River S-R Plot

Shepherd Recruitment Function

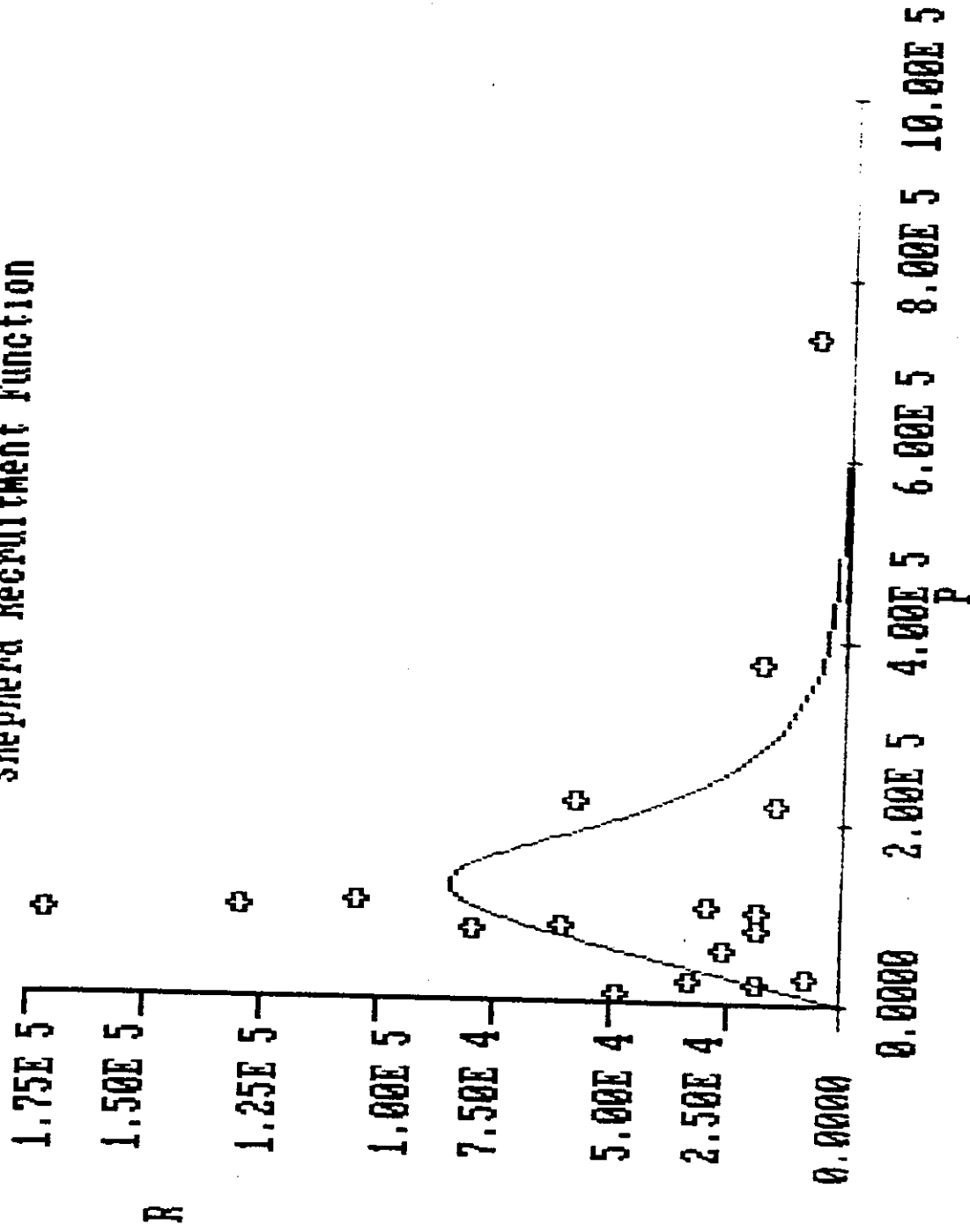


Figure 10- Edisto River S-R Plot

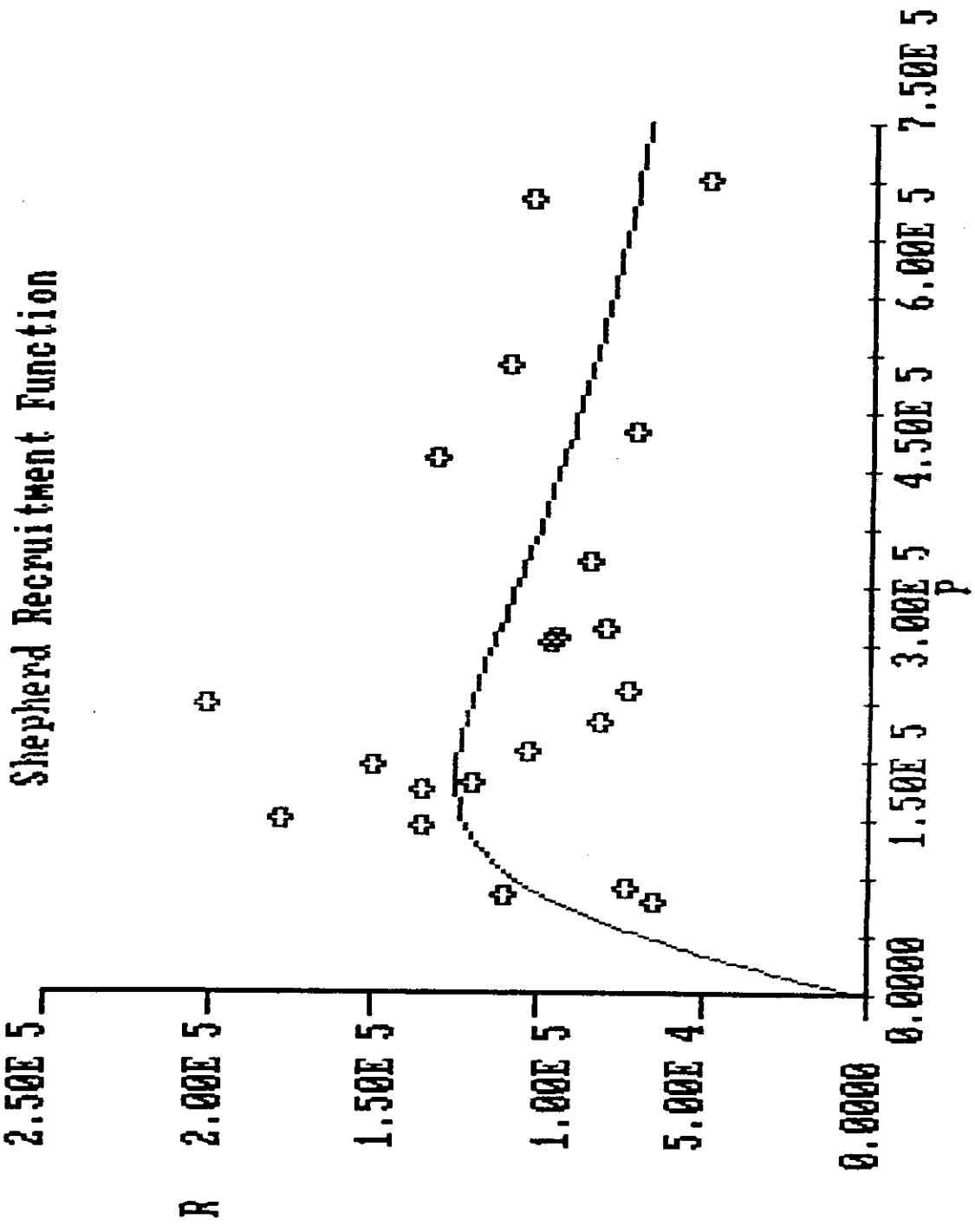


Figure 11- Savannah River S-R Plot

Shepherd Recruitment Function

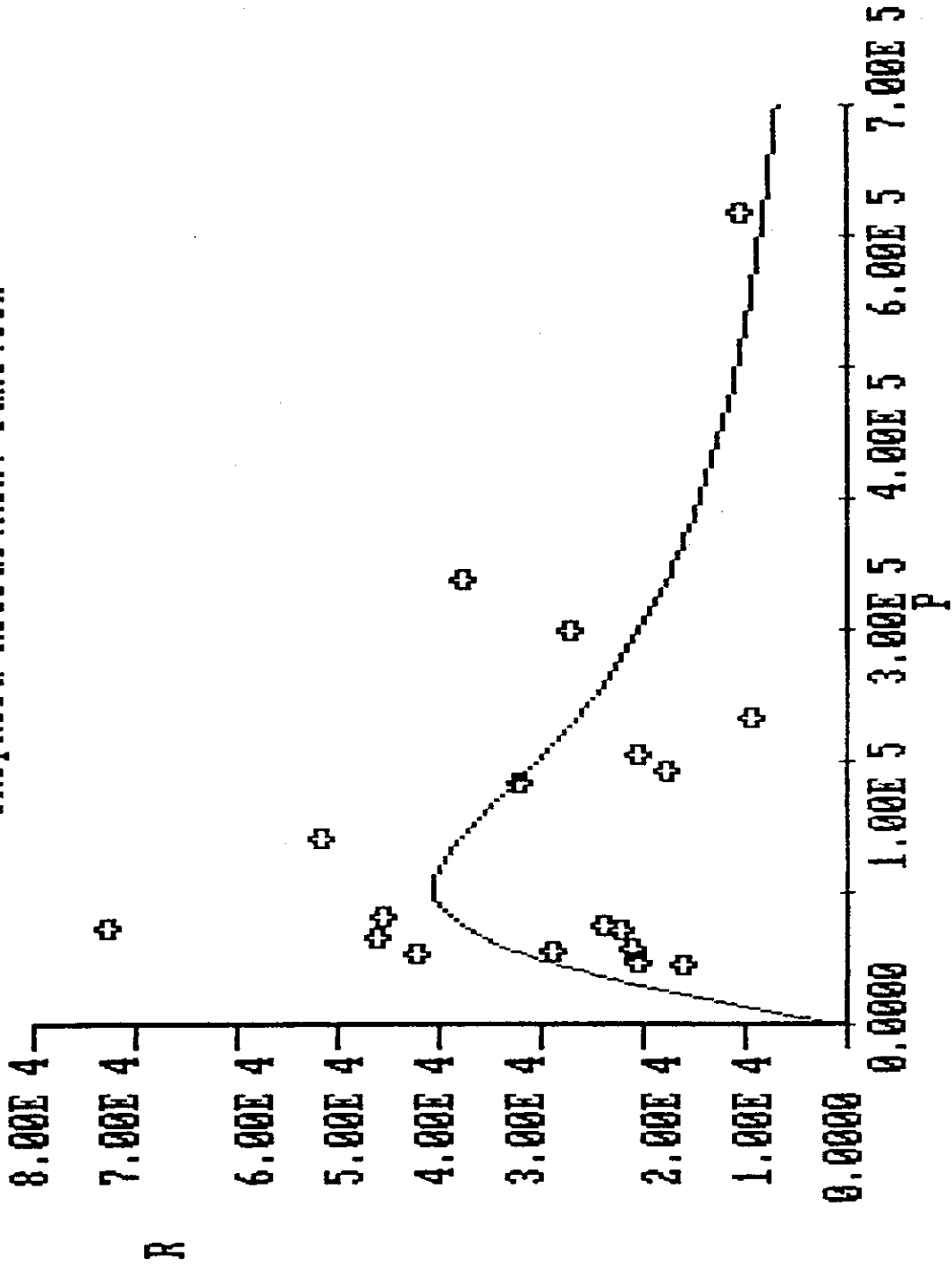


Figure 12- Altamaha River S-R Plot

Shepherd Recruitment Function

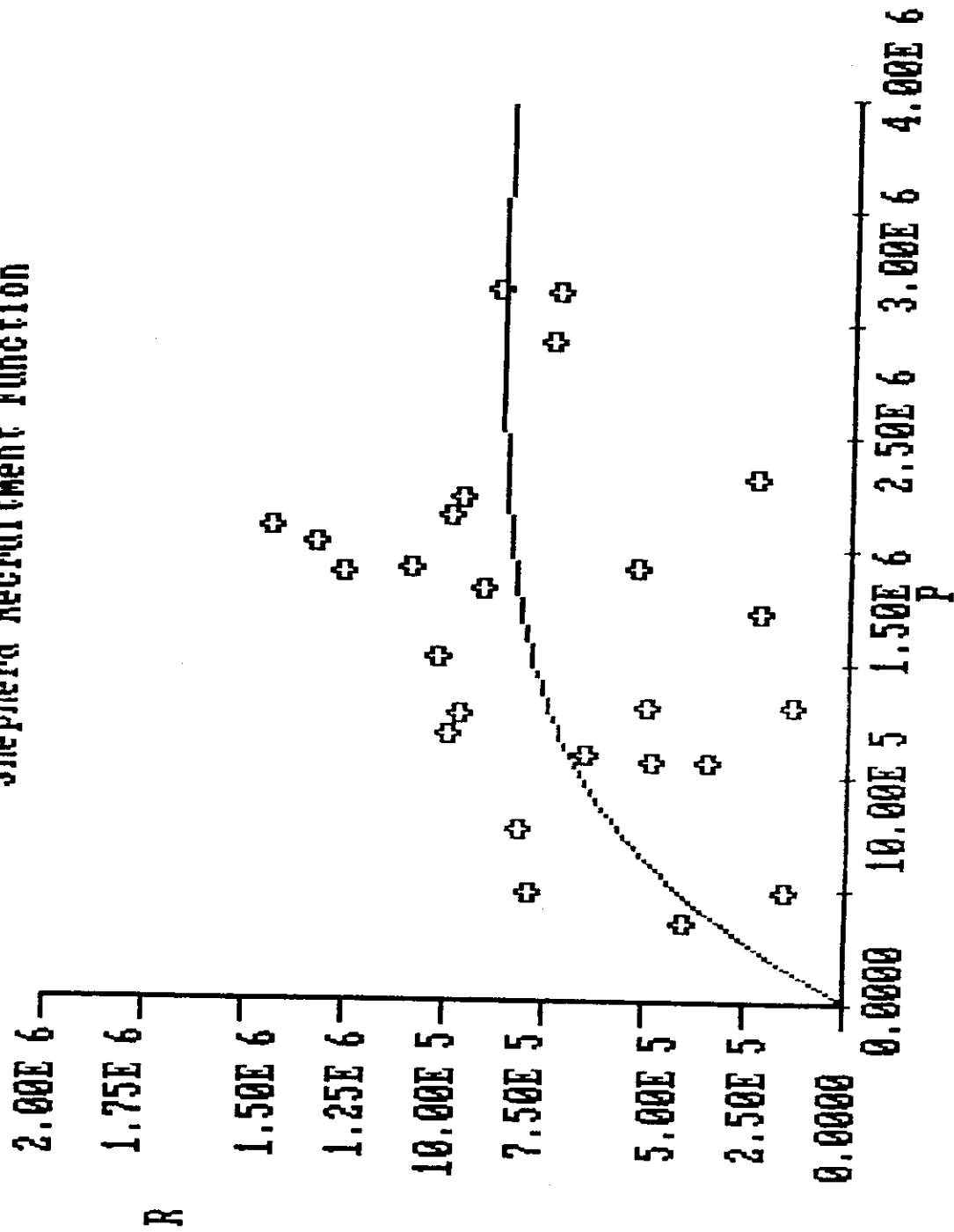


Figure 13- St. John's River S-R Plot

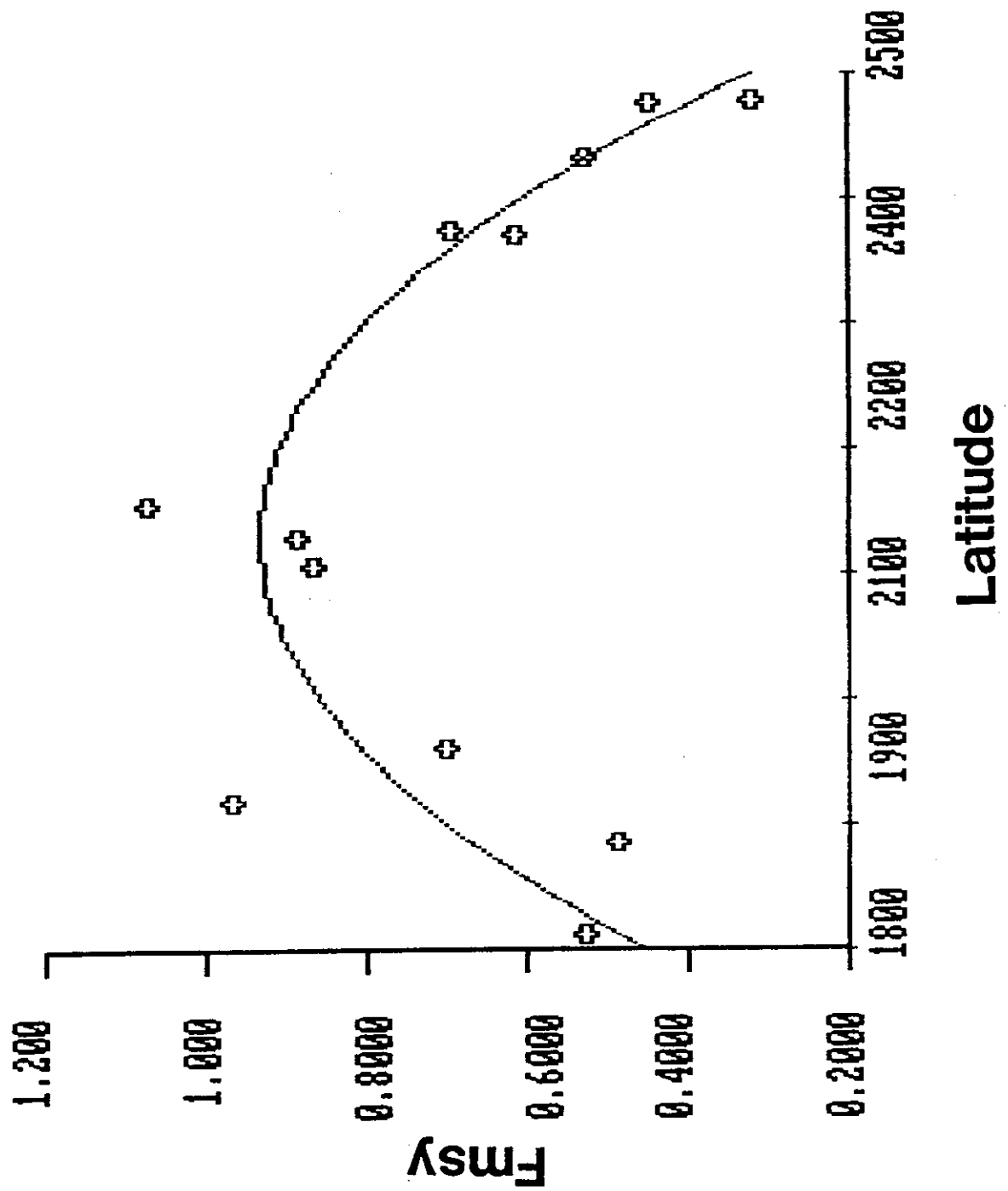


Figure 14 - Shad Fishing Rates vs. Latitude

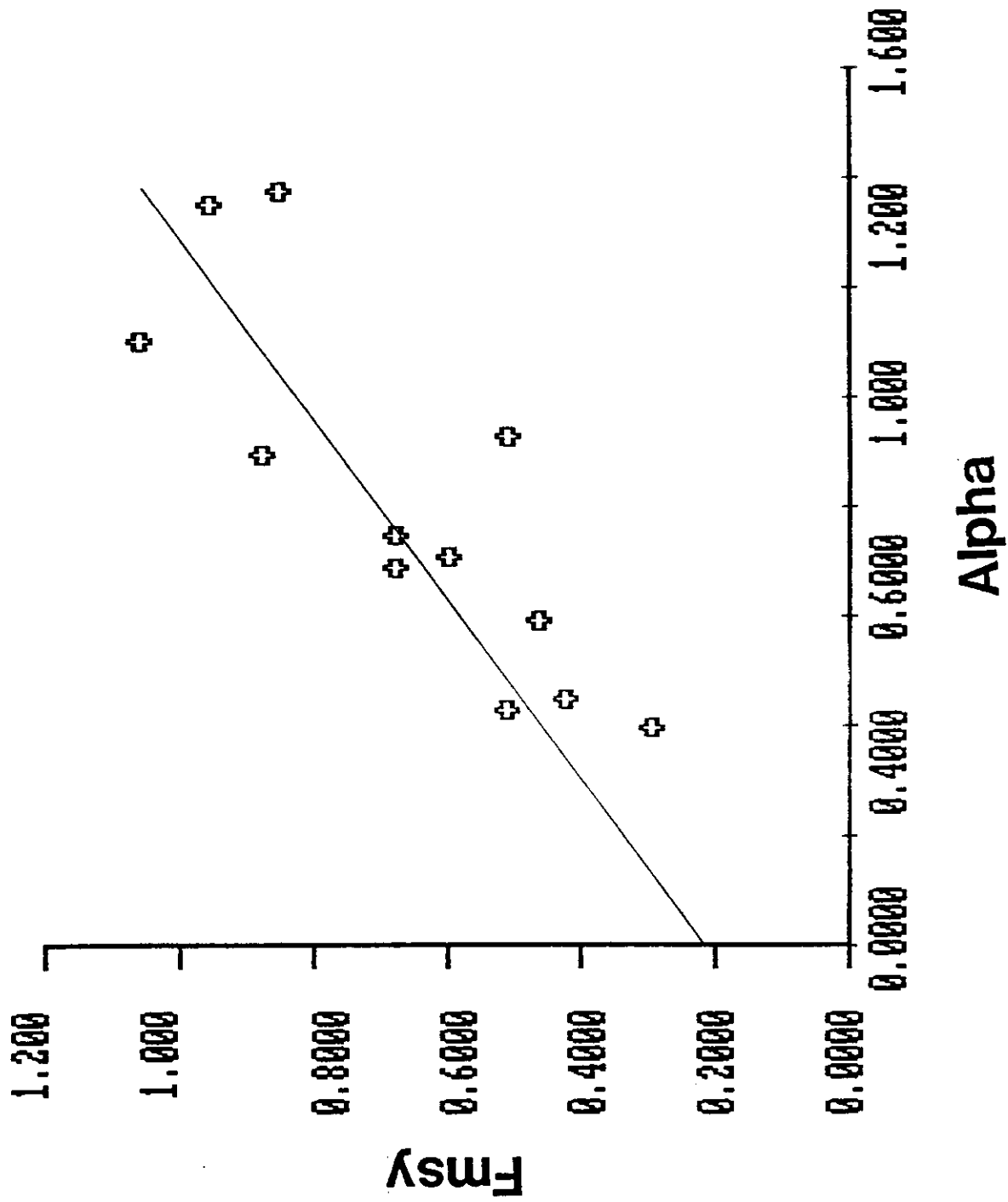


Figure 16- Shad Fishing Rates vs. Slope of S-R Model

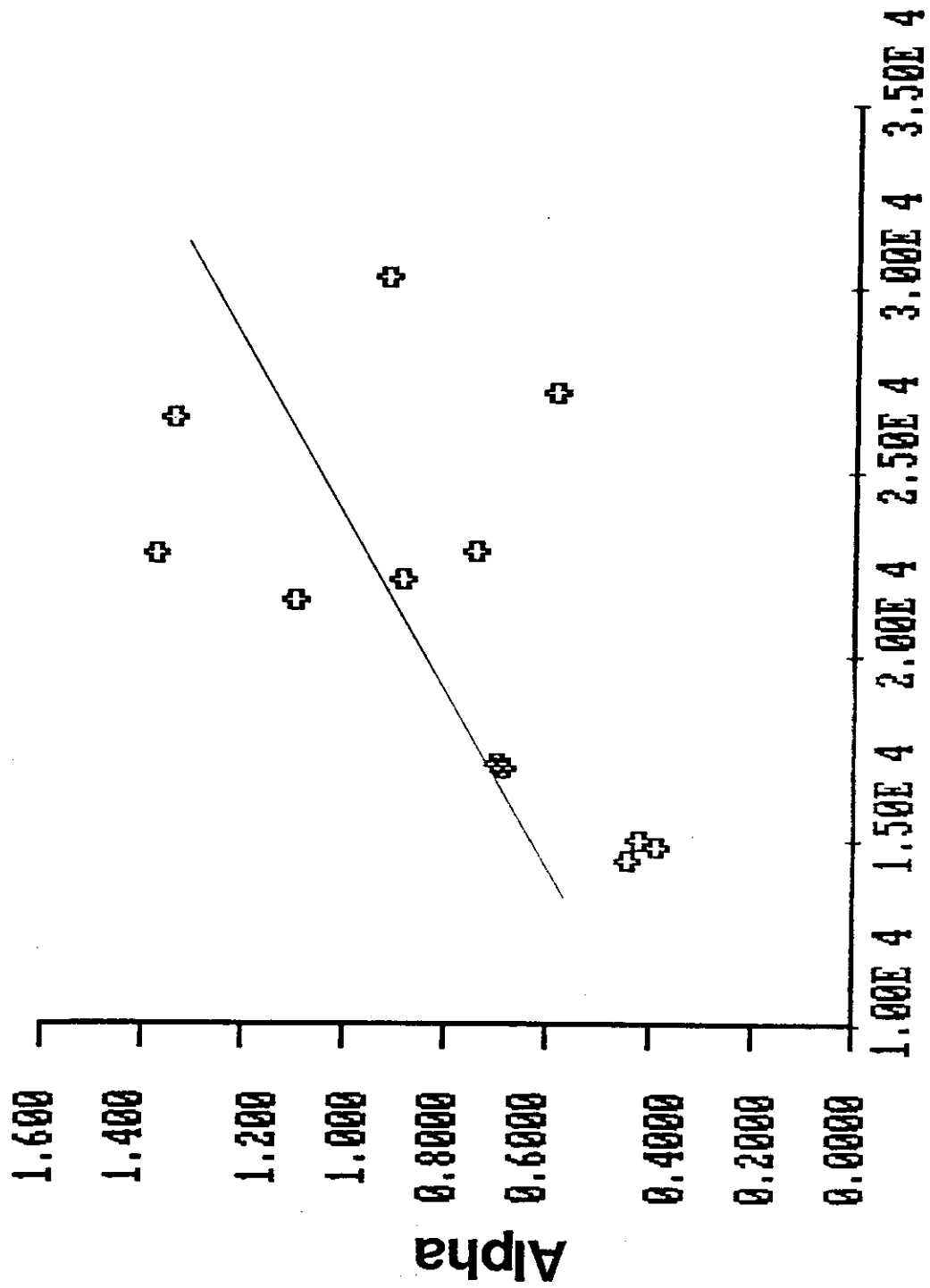
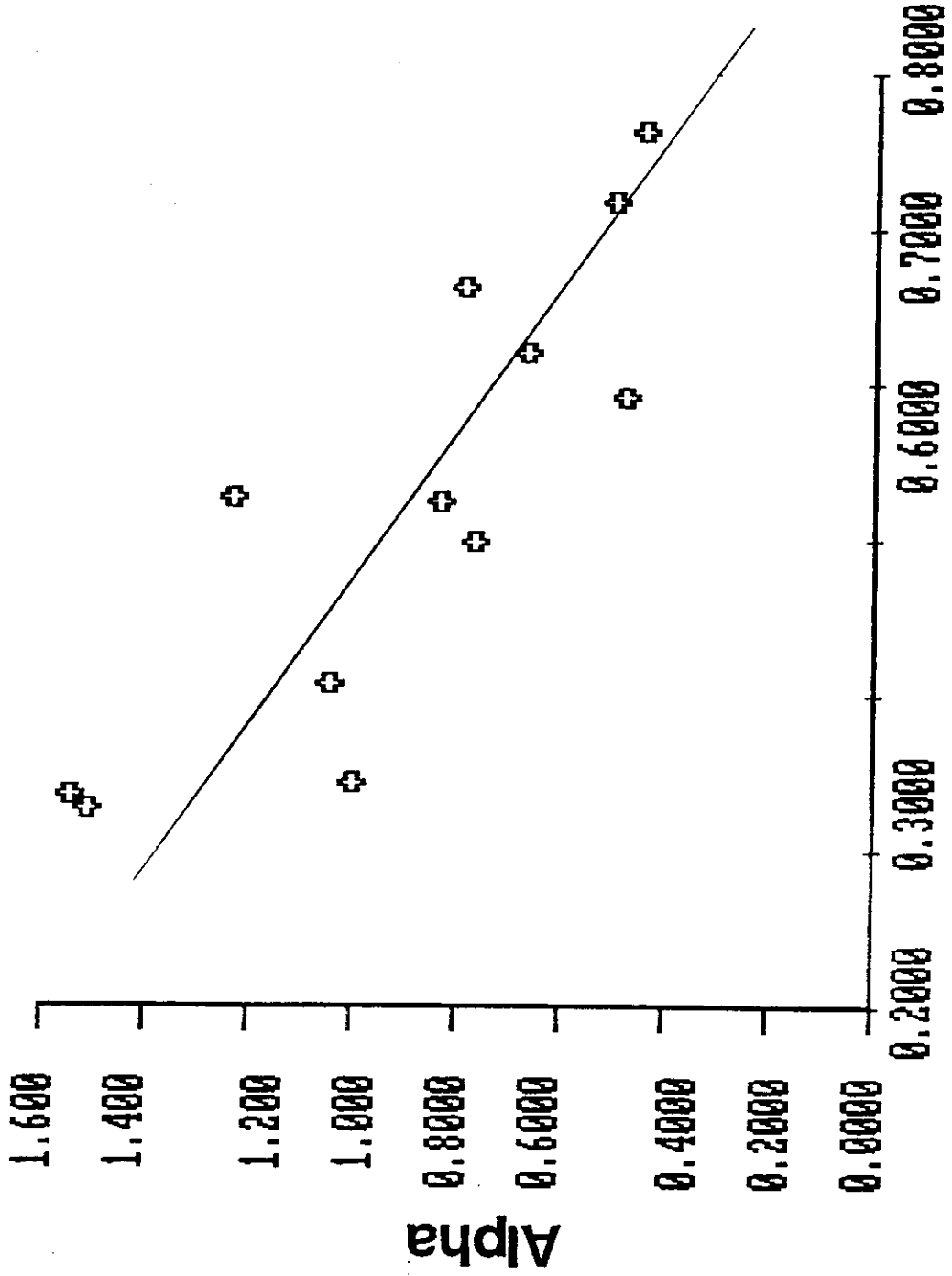


Figure 17- Alpha vs. Fecundity in Shad Rivers



FlowCV

Figure 18-- Alpha vs. Flow Variation

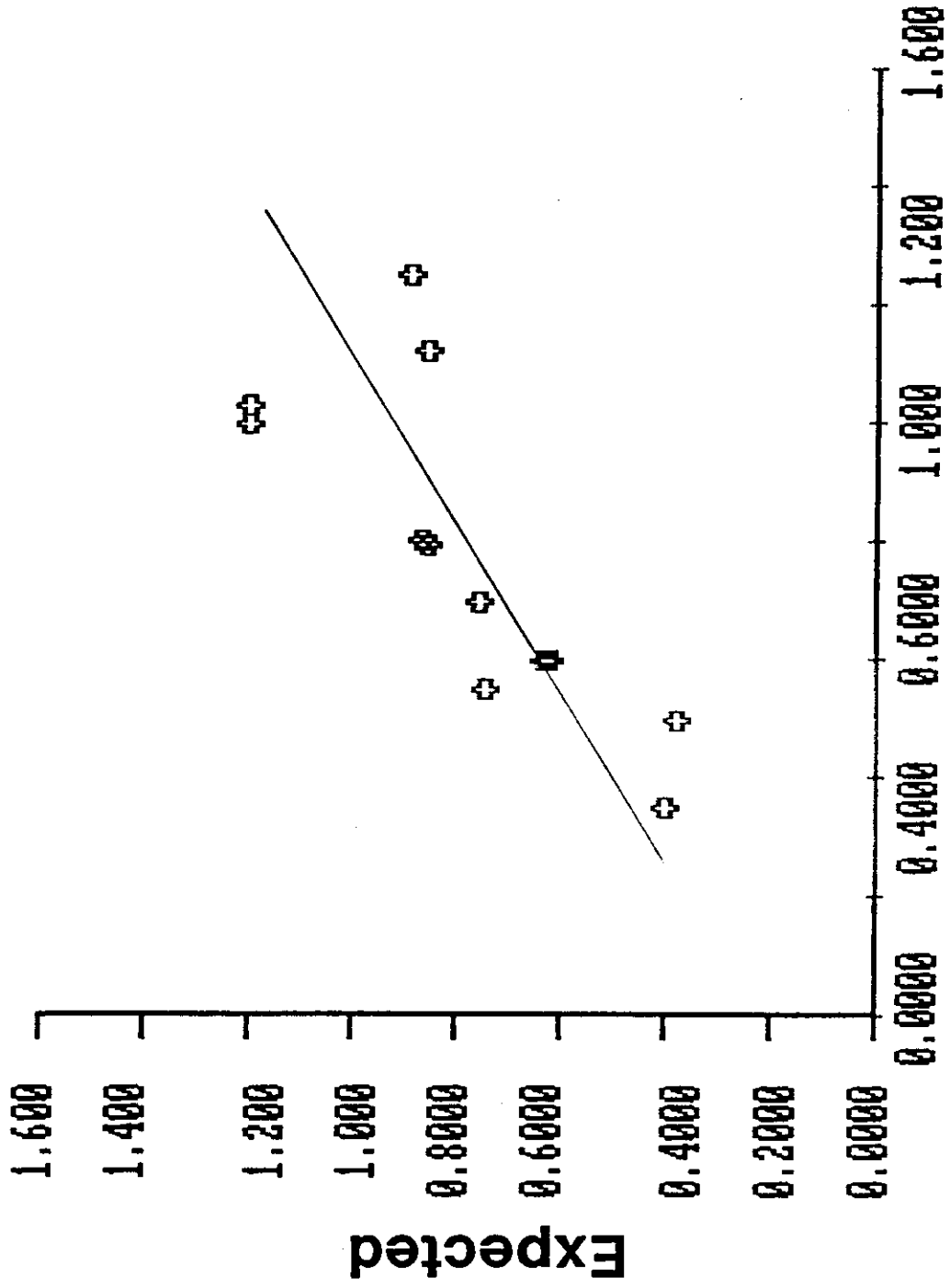


Figure 19- Observed vs. Predicted Fmsv in Chad River

APPENDIX 1

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

Year	1/ Pawcatuck River RI.		2/ Connecticut River CT.		Hudson River NY.		Delaware River NY, NJ, PA.	
	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³
1950	-	-	-	-	1280	1308	-	-
1951	-	-	-	-	1351	2311	-	-
1952	-	-	-	-	1185	2604	-	-
1953	-	-	-	-	1026	2645	-	-
1954	-	-	-	-	915	3178	-	-
1955	-	-	-	-	678	4343	-	-
1956	-	-	-	-	1559	5021	-	-
1957	-	-	-	-	464	4627	-	-
1958	-	-	-	-	324	3248	-	-
1959	-	-	-	-	240	3938	-	-
1960	-	-	-	-	217	2470	-	-
1961	-	-	-	-	184	2106	-	-
1962	-	-	-	-	238	1916	-	-
1963	-	-	-	-	286	1407	-	-
1964	-	-	-	-	282	785	-	-
1965	-	-	-	-	254	1041	-	-
1966	-	-	529	529	270	555	-	-
1967	-	-	768	768	319	834	-	-
1968	-	-	929	929	287	1136	-	-
1969	-	-	1766	1766	242	1132	-	-
1970	-	-	1900	1900	213	1041	-	-
1971	-	-	1950	1950	203	825	243.4	292.2
1972	-	-	768	768	303	1377	84.6	118.3
1973	-	-	511	511	462	1168	26.0	170.6
1974	0	0	1408	1408	610	956	40.3	201.4
1975	24	87	1136	1136	681	773	14.3	219.0
1976	214	786	2001	2001	412	754	-	-
1977	181	663	952	952	297	621	-	-

APPENDIX 1 continued

Year	1/ Pawcatuck River RI.			1/ Connecticut River CT.			2/ Hudson River NY.			2/ Delaware River NY, NJ, PA.		
	Recruitment N x 10 ³	Spawners lbs x 10 ³	Spawners ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Spawners ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Spawners ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Spawners ³
1978	140	513	449	966	345	2006	-	-	-	-	-	
1979	312	1146	494	1141	396	1517	84.6	181.5	84.6	181.5	181.5	
1980	386	1416	369	1569	285	3043	162.7	339.7	162.7	339.7	339.7	
1981	326	1198	302	1348	-	-	223.9	694.1	223.9	694.1	694.1	
1982	219	803	267	2305	-	-	199.1	1105.5	199.1	1105.5	1105.5	
1983	280	1026	-	-	-	-	441.3	396.8	441.3	396.8	396.8	
1984	-	-	-	-	-	-	322.8	422.3	322.8	422.3	422.3	
1985	-	-	-	-	-	-	261.3	707.4	261.3	707.4	707.4	
1986	-	-	-	-	-	-	264.3	1206.1	264.3	1206.1	1206.1	

1/ Recruitment was Adjusted for June Flow Effects

2/ Hudson River Data Dates Back to 1915

APPENDIX 1 continued

Year	Susquehanna River Maryland, PA.		Nanticoke River Maryland, Delaware		James River Virginia		Chowan River N.C.	
	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³
1944	729.4	2131	28.0	258	-	-	-	-
1945	789.8	923	30.5	71	-	-	-	-
1946	1095.5	694	27.0	53	-	-	-	-
1947	1312.0	800	26.8	95	-	-	-	-
1948	1255.3	2480	52.8	99	-	-	-	-
1949	1137.5	1806	55.3	126	-	-	-	-
1950	987.5	1669	55.8	118	-	-	107.9	76.5
1951	1037.5	3615	51.5	263	-	-	98.9	84.9
1952	1273.3	3365	31.8	292	-	-	88.5	251.3
1953	1268.0	3173	84.5	301	-	-	67.8	249.5
1954	887.3	3504	78.8	632	-	-	63.0	239.7
1955	805.3	1888	78.0	580	-	-	76.6	147.4
1956	651.3	2138	76.6	1059	-	-	96.6	181.8
1957	503.0	5069	74.8	788	-	-	111.7	178.1
1958	192.5	2466	55.3	169	-	-	128.7	95.5
1959	129.8	2847	25.8	419	-	-	142.2	88.8
1960	96.0	1281	21.8	408	-	-	124.0	101.7
1961	129.5	2593	35.5	402	-	-	94.3	185.5
1962	80.8	625	20.6	292	-	-	108.3	172.9
1963	141.0	580	38.0	175	-	-	101.9	195.4
1964	108.5	149	29.8	201	-	-	57.1	363.3
1965	100.3	98	49.6	160	-	-	46.7	412.4
1966	112.5	380	17.6	75	-	-	54.4	36.5
1967	115.5	446	21.3	209	-	-	54.7	206.8
1968	80.3	300	41.8	243	-	-	37.1	301.7
1969	48.6	187	73.0	340	-	-	26.6	29.0
1970	37.0	213	-	-	732.5	1689.0	26.3	47.6
1971	36.8	247	-	-	-	-	35.5	56.7
1972	49.3	235	-	-	627.7	953.0	47.7	226.8
1973	-	-	-	-	-	-	53.7	57.8
1974	-	-	-	-	287.5	345.3	40.6	51.0
1975	-	-	-	-	213.8	341.2	29.7	27.9
1976	-	-	-	-	532.7	219.5	38.7	46.0
1977	-	-	-	-	182.2	148.6	62.4	59.6

APPENDIX 1 continued

Year	Susquehanna River Maryland, PA.		Nanticoke River Maryland, Delaware		James River Virginia		Chowan River N.C.	
	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ³ lbs x 10 ³	Recruitment N x 10 ³	Spawners ² lbs x 10 ³
1978	-	-	-	-	576.2	246.6	90.1	136.6
1979	-	-	-	-	241.0	123.0	98.9	88.8
1980	-	-	-	-	334.7	68.6	-	24.2
1981	-	-	-	-	92.7	12.5	-	58.1
1982	-	-	-	-	36.7	146.8	-	76.3
1983	-	-	-	-	117.4	174.7	-	193.7
1984	-	-	-	-	139.5	472.1	-	282.3
1985	-	-	-	-	55.5	22.0	-	-

APPENDIX 1 continued

Year	Neuse River N.C.		Tar-Pamlico River N.C.		Cape Fear River N.C.		Pee Dee River S.C.	
	Recruitment N x 10 ³	Spawners lbs x 10 ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Recruitment N x 10 ³	Spawners lbs x 10 ³
1950	-	-	138.7	128.2	16.2	31.8	-	-
1951	-	-	135.7	143.4	16.6	35.3	-	-
1952	130.4	107.3	121.1	395.1	14.8	75.1	17.0	19.9
1953	122.4	126.5	86.4	387.1	10.2	70.5	20.3	10.1
1954	113.3	166.8	77.3	381.8	9.3	69.6	25.7	3.05
1955	115.7	225.2	97.9	230.9	12.1	39.2	28.2	0.52
1956	126.7	228.6	126.5	283.5	17.6	48.0	29.9	0.25
1957	121.0	245.5	133.8	280.8	20.6	47.5	29.9	1.18
1958	129.8	211.2	143.4	151.1	19.4	25.9	33.7	1.13
1959	174.4	203.2	219.8	139.1	22.2	23.7	31.7	1.02
1960	206.4	184.0	275.8	159.7	23.6	27.8	23.7	1.42
1961	220.0	276.8	218.3	287.1	9.8	47.2	18.0	1.34
1962	207.8	232.5	220.0	283.2	13.4	62.9	15.8	1.48
1963	235.0	177.0	242.8	270.2	28.8	56.9	15.0	2.00
1964	248.0	500.8	250.3	374.0	35.2	49.6	16.9	65.2
1965	194.2	529.6	225.3	996.9	37.5	109.1	19.4	51.2
1966	218.6	572.9	174.5	256.8	42.2	18.0	21.4	46.6
1967	205.9	428.0	112.8	459.6	42.7	10.8	23.7	123.8
1968	213.4	457.5	86.4	484.9	24.1	74.9	33.1	51.0
1969	200.0	836.4	73.4	614.9	14.9	91.9	45.9	130.9
1970	186.6	187.8	51.0	243.6	11.8	102.3	51.9	438.9
1971	207.5	693.3	31.3	361.8	8.2	106.9	55.9	320.8
1972	205.9	437.1	34.4	199.3	13.5	154.9	54.1	228.5
1973	210.5	608.8	45.7	170.2	23.3	66.4	60.4	64.3
1974	222.8	562.0	33.5	141.4	27.6	31.4	98.9	107.0
1975	212.7	388.0	34.8	100.9	19.0	38.2	128.4	99.1
1976	212.8	677.9	52.4	67.4	19.4	12.2	117.3	101.0
1977	223.1	613.1	61.6	44.0	21.3	27.3	77.3	67.4
1978	230.4	508.4	76.6	75.3	19.3	43.9	46.5	8.01
1979	-	394.8	106.3	30.7	-	93.2	39.9	27.4
1980	-	471.3	-	30.3	-	19.8	41.7	26.6
1981	-	484.5	-	91.0	-	17.6	38.9	22.7
1982	-	436.1	-	106.2	-	14.5	39.3	57.8
1983	-	482.5	-	98.5	-	11.8	36.6	58.9
1984	-	476.3	-	209.0	-	11.1	30.2	67.9
1985	-	-	-	-	-	-	29.4	137.6
1986	-	-	-	-	-	-	33.9	49.6

Appendix 1 (Continued)

Year	Edisto River N.C.		Savannah River Georgia		Altamaha River Georgia	
	Recruitment N x 10 ³	Spawners lbs x 10 ³	Recruitment N x 10 ³	Spawners lbs x 10 ³	Recruitment N x 10 ³	Spawners lbs x 10 ³
1960	29.8	109.5	-	-	45.7	82.9
1961	-	-	-	-	42.5	55.0
1962	61.1	86.0	-	-	46.6	67.7
1963	105.2	112.0	66.3	79.8	73.2	75.4
1964	172.0	97.0	74.8	91.0	52.2	143.4
1965	130.8	102.7	136.4	175.6	37.9	339.7
1966	79.8	81.4	201.8	249.1	27.7	301.6
1967	59.1	224.5	179.8	151.3	18.3	194.3
1968	19.1	377.0	121.6	181.1	10.9	617.7
1969	8.9	735.4	135.9	144.4	9.8	233.4
1970	-	410.4	96.7	302.5	-	-
1971	-	215.2	104.2	682.8	-	-
1972	-	231.3	51.0	701.2	-	-
1973	49.5	10.8	73.9	260.2	20.8	48.7
1974	33.6	26.1	110.4	541.8	16.4	47.1
1975	8.8	30.3	150.2	197.8	22.6	72.9
1976	22.3	-	132.4	461.1	24.1	76.5
1977	19.1	23.8	110.9	85.4	21.2	59.4
1978	15.7	221.3	104.5	208.8	32.6	185.3
1979	19.9	102.6	82.7	233.9	29.0	56.9
1980	27.3	61.8	72.2	483.3	20.7	205.5
1981	19.8	82.8	85.3	372.9	-	-
1982	-	64.1	80.5	315.0	-	-
1983	-	42.2	96.5	307.0	-	-
1984	-	64.6	-	-	-	-
1985	-	110.6	-	-	-	-
1986	-	65.5	-	-	-	-

Appendix 1 (Continued)

Year	St. John's River Florida	
	Recruitment N x 10 ³	Spawners lbs. x 10 ³
1950	1095902	661122
1951	1277221	978363
1952	760642	832974
1953	484496	802782
1954	1187297	1007829
1955	2220316	972245
1956	1828032	924419
1957	1525318	1035505
1958	2098078	1450362
1959	2026838	1340246
1960	1915821	1106188
1961	1894080	1277365
1962	3141296	894501
1963	3136342	745316
1964	2144468	1001394
1965	2914929	753117
1966	1914040	528518
1967	1308868	510522
1968	2311106	241745
1969	1727567	235127
1970	1069505	360612
1971	1315319	142842
1972	492828	155386
1973	351206	410743
1974	1060148	497156

