Population dynamics of the American shad (*Alosa sapidissima*) in the Connecticut River, 1940 - 1977

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INTRODUCTION

From mid-March through early April, adult American shad (*Alosa sapidissima*) leave the ocean and ascend the Connecticut River to spawn. The shad is considered the most important commercial finfish in Connecticut with an annual monetary value of approximately $7,000,000 (Bampton, 1964). Accordingly, the annual shad runs in the Connecticut River have been extensively examined during the last three decades (principally, Fredin, 1954; Walburg, 1961, 1963; and Leggett, 1969, 1976, 1977). However, studies specifically concerned with the effects of commercial and sport fishing on growth and recruitment of adult shad are lacking.

Previous research (Leggett and Whitney, 1972) has shown that the onset of the shad migration appears to be governed by water temperature. Spawning activity, which is also influenced by water temperature, usually begins during late May and extends through June. The young shad spend from four to six months in the river before descending to the ocean sometime during October and November. Adult shad return to the ocean shortly after spawning.

Historically, shad have spawned in the Connecticut river as far north as Bellows Falls, Vermont, 274 km from the river mouth (Stevenson, 1898). However, in 1798 a dam was constructed at Turners Falls, Massachusetts, which precluded any further spawning beyond km 185. In 1900 the construction of a 17 m high dam at Holyoke, Massachusetts further restricted spawning to a 97 km stretch between Haddam, Connecticut and the base of the Holyoke Dam. A fish lift facility at Holyoke began operation in 1955, and for the past 22 years spawning had again occurred as far north as Turners Falls. Since 1975, a large portion of each year's spawning stock has been transported over the Holyoke Dam by the fish lift facility and allowed to spawn between Holyoke and the next dam at Turners Falls, Massachusetts. Thus, the size of the shad runs during the 1980's will largely depend upon spawning success and subsequent recruitment from above the dam.

There may be many problems associated with the Holyoke facility, including increased adult and juvenile mortality due to the absence of downstream migrant facilities. An increase in adult mortality may occur due to their entrapment in the dam's canal system, and thus eliminating the possibility of repeat spawners. In addition, juveniles produced in the Holyoke pool will have to emigrate by passing through the turbines, over the dam, or through a complex canal system. This may result in substantial juvenile mortality, and could reduce the potential for good recruitment in future years. These potential problems have not been addressed in previous research. It should be emphasized, however, that the effects of fishing and the Holyoke Dam can be properly evaluated only after we have obtained better insight into the dynamics of the shad population. A comprehension of the shad's population dynamics presents a challenge to fishery science, both as a scholarly endeavor to understand the mechanisms of natural regulation, and as a practical matter to develop sound management strategies.

The objectives of the present study are:

1) to estimate the parameters of growth, natural mortality, and fishing mortality using stock estimates and age composition data;

2) to compute estimates of equilibrium yield (weight of the catch) at various combinations of fishing mortality and natural mortality while maintaining recruitment and growth at a constant;

3) to examine the relationship between parent stock and recruitment, and to estimate the level of escapement which will result in a maximum surplus of virgin recruits in the next generation;

4) to determine the fishing rates which produce both a maximum sustainable yield (MSY) and optimum yield per expenditure of fishing effort for the commercial fishery;

5) to examine the relationship between changes in the numbers of adult shad transported over the Holyoke Dam and corresponding alterations in the magnitude of adult natural mortality;

6) to present a working hypothesis as to the mechanisms of density-dependent mortality based on existing data; and

7) to provide specific management recommendations for the adult shad population in the Connecticut River.

Estimates of growth, natural mortality, and fishing mortality are integral components in the resolution of the stock assessment problem. However, determination of the reproductive relationship between stock and recruitment is perhaps the most essential, yet the most difficult problem facing scientists concerned with fishery management. It is important because, annual variation in recruitment greatly influences the magnitude of the catch at a given rate of exploitation. It is an arduous problem because an adequate study of stock-recruitment requires a long series of population estimates. Furthermore, the reproduction and recruitment mechanisms are probably the least understood areas in fishery science, mainly because the larval and juvenile stages, as separate entities, are not the object of fisheries management. Information concerning food habits, growth and natural mortality of post-larval shad is scarce and difficult to obtain in the field. Thus, the greatest obstacle to effective management of Connecticut River shad involves the resolution to the stock-recruitment problem. Once the reproductive mechanism is better understood, an effective management strategy can be developed based on the estimated level of female escapement that would produce the greatest surplus of recruits, and thus the best yield to the fishery. Fishing effort can then be adjusted allowing the optimum number of females to reach the spawning grounds.

Although many researchers have alluded to the existence of density-dependent mortality during the early life history of the shad, a hypothesis concerning its mechanism and the influence exerted by the commercial fishery upon recruitment have not been investigated in previous studies.

In the Connecticut River, attempts to obtain better insight into the population dynamics of the American shad have been approached in several ways. Fredin (1954) estimated the adult shad population for the years 1935-1951 with the use of a single mark-recapture study. In addition, he provided detailed information concerning fishing effort and catch per effort by the commercial fishery. The relationship between size of the parent stock and subsequent recruitment has been reported by Walburg (1963) and Leggett (1976). The comprehensive study by Leggett not only included data on stock-recruitment, but also provided much needed information on stock abundance, migration patterns, age composition, sex ratio, natural mortality, fishing mortality, and an appraisal of the adult shad population for the years 1965-1973. From 1965 through 1973, an extensive study of the juvenile life history was conducted below the Holyoke Dam by Marcy (1976). Since 1968, investigations of all life stages from above the Holyoke Dam have been undertaken by the Massachusetts Cooperative Fishery Unit (Watson, 1968, 1970; Sherer, 1974; and Foote, 1976). Since 1974, the Connecticut Department of Environmental Protection (D.E.P.) has assumed responsibilities for the shad study from below Holyoke (Jones, et al. 1976). In the interest of space, I have presented only a partial listing of the literature that pertains to the population dynamics of Connecticut River shad. A more comprehensive literature review can be found in Leggett (1976) or in Marcy (1976).

Because the study of shad population dynamics requires a long series of reliable data, it was necessary to include in my analysis some of the data presented by Fredin (1954) and Leggett (1976). While reviewing their data, I discovered some general inconsistencies either in the methods of determining certain parameters or in the interpretations. As a result, my interpretations and conclusions respecting these data differ from those of Fredin and Leggett mainly because they are predicated upon different hypotheses. Since the exact interrelationship among many factors is unknown hypothesis testing is the only method which provides a basis for action. Consequently, several hypotheses advanced herein will require further research and they may have to be abandoned or revised if further data show them to be inadequate.

In this report, the economic objectives associated with maximizing the margin between the value of the catch and the cost of operations are not considered. Their analyses would entail an examination of the relations between the magnitude of the stock and the amount of effort involved in taking the desired catch. This would involve a number of important but complex questions unrelated to the biological phenomena which form the basis for this report. These economic problems are certainly worthy of critical analyses and should be subjected to investigation in a separate report.

ASPECTS OF THE COMMERCIAL AND SPORT FISHERIES

The commercial fishing season usually starts during the second week of April and continues until the shad run declines in the middle of June. Walburg and Nichols (1967) reported that prior to World War II haul seines and pound nets, to a lesser extent, were the traditional gear employed to catch shad in the river. However, during the last three decades fishermen have favored drift gill nets, ostensibly because the gill net is less cumbersome and requires fewer man hours to operate. The typical gill net is 35 to 50 meshes deep, varies in length from 183 to 274 m, and varies in stretch mesh size from 13.7 to 14.6 cm (Walburg and Nichols, 1967). These mesh sizes tend to select for the longer and heavier females, which, because of their roe, are worth more at the market place.

All gill nets are made of multifilament, since monofilament nets are forbidden by law. Most of the fishing occurs after dusk when the heavy nylon nets become invisible to the fish and thus reach optimal efficiency. During the last fifty years, technological advances in gear design, which could have had an important effect on gear efficiency, have been absent from the commercial fishery. Drift gill netting for shad is conducted today in essentially the same manner as it was forty years ago (Fredin, 1954). Fishing is permitted from Sunday through Thursday each week. All commercial fishermen are required by law to report their daily catch annually to the Connecticut Department of Environmental Protection.

After passing the gauntlet of gill nets in the lower river, the surviving shad enter the sport fishing areas further upriver. Most sport fishing has been concentrated around the Enfield Dam at Suffield, Connecticut. Nichols and Tagatz (1960) found that sport fishermen take shad using the following techniques: 1) trolling lead bodied jigs from boats; 2) drifting metal spoons from bridges; and 3) casting gold hooks garnished with colored beads from the river bank.

The sport fishing season opens on the third Saturday of April and usually closes on the last Sunday of June. The daily creel limit is six fish per angler. According to a creel census conducted by Nichols and Tagatz (1960), male shad constituted 59% of the catch during 1957 and 53% during 1958. Leggett (1976) conducted creel surveys during the years 1965-1973 and revealed no significant deviation from a 50:50 sex ratio for the entire sport fishery. However, for the access area at Enfield , his results did show a selection in favor of females (41%/59%).

CRITICAL REVIEW OF THE STOCK ESTIMATES, FISHING EFFORT AND ADJUSTED CATCH, 1935-1965.

An examination of the changes in yield (weight of the catch) with corresponding alterations in fishing effort requires information on both the types of gear used and the numbers of fishing days expended in the fishery. From these data, a measurement of fishing effort must be developed in equivalent units to insure that total effort is proportional to the instantaneous rate of fishing mortality (F), and that the catch per unit of effort is commensurate with the population size.

For the commercial shad fishery, Fredin (1954) established the standard fishing unit day (SFU) as a simple but effective measure of fishing effort. He defined one SFU as equivalent to one day's fishing by a single drift gill net. From the catch reports, 1935 - 1951, Fredin analyzed the catch efficiency of haul seines and pound nets, since the catch per one day's fishing may not have been comparable among the three gear types. He concluded that haul seines and pound nets caught 60% and 30% respectively, more shad per day's fishing than drift gill nets. Accordingly, by defining the fishing power of a drift gill net as 1.0 SFU, fishing power of a haul seine was tantamount to 1.6 SFU, and that for a pound net was equivalent to 1.3 SFU. For each year, Fredin (1954) then converted the total number of fishing days for each gear type to equivalent SFU, the sum of which was synonymous to the total fishing effort. Estimates of annual fishing effort are presented by Fredin (1954, Table 4, p. 251) for the period, 1935 - 1951.

The argument may be offered that a day's fishing is not an accurate measure of fishing time, because the average number of fishing hours varies during the year, as well as between years. However, by expressing fishing time as fishing unit days, Fredin was able to quantify, in comparable units, the amount of fishing effort pursued by drift gill nets, pound nets, and haul seines.

Fredin (1954) also attempted to estimate the shad run from 1935-1950 using a single mark-recapture study. During the spring of 1951, 633 fish were captured at the river mouth, tagged with Petersen disk tags, and released to continue their upriver migration. A 50 cent reward was given for each tag returned at the end of the season. The commercial fishermen reported taking 100,967 fish, 359 of which were tagged. The size of the 1951 population was computed to be 178,072 individuals after employing the following equation:

$$N_x = M_x C_x / R_x \qquad (1)$$

where N_x = estimate of the population in year x

M_x = total number of fish tagged in year x

R_x = total number of fish recaptured in year x

C_x = reported catch in year x

From the stock size, escapement, and fishing effort (SFU), Fredin then estimated the catchability coefficient (p) and the inverse of the coefficient ($q = 1 - p$) of one SFU using the equation:

$$q^n N = E \qquad (2)$$

where $q = 1 - p$ = the proportion of the stock remaining after the utilization of one SFU (constant)

p = catchability coefficient = the proportion of the stock removed after utilizing one SFU (constant)

N = population estimate

E = escapement = the estimated population minus the reported catch

n = total fishing effort (SFU)

By rearranging equation (2) with respect to (q): $q = \sqrt[n]{E/N}$, the inverse constant (q) was calculated as 0.999675, and thus the catchability coefficient (p) was 0.000325. Fredin then concluded that 0.0325 percent of the stock was removed after utilizing one SFU.

Given the constant (q) as well as estimates of effort and reported catches for the years, 1935-1950, Fredin attempted to compute the size of the annual shad run by utilizing the following equation:

$$N_x = C_x/(1-0.999675^{n_x}) \qquad (3)$$

where N_x = population estimate in year x

C_x = reported catch in year x

n_x = total fishing effort (SFU) in year x.

From 1935 through 1951, the estimates of the shad run, fishing effort, annual fishing rate, and escapement are reported in Fredin (1954, Table 6, p. 255).

It is important to note that equation (3) could have provided accurate estimates of the shad runs (1935-1950) only if the following data were unbiased: the reported catches; the 1951 population estimate; and the estimates of the catchability coefficient (p), and it's inverse (q). The accuracy of Fredin's 1951 population using the mark-recapture technique depends on a number of conditions as described by Ricker (1975): 1) the marked fish suffer the same natural mortality as the unmarked fish; 2) the marked fish are equally vulnerable to fishing as the unmarked fish; 3) the tagged fish do not lose their marks; 4) the marked fish become randomly distributed among the unmarked fish; and 5) all tags are recognized and reported. These conditions would have also affected Fredin's estimates of (p) and (q) as well. Whether Fredin (1954) satisfied any of these assumptions is not known, since no pilot study was conducted to account for these sources of bias. In addition, Fredin assumed among other things that the reported catches were entirely reliable. The accuracy of Fredin's stock estimates was examined later by Leggett (1976) as discussed later in this paper.

In Fredin's analysis, for equation (3) to provide a precise estimate of the shad run, the catchability coefficient (p) must be constant with time, such that the instantaneous fishing mortality rate (F) is directly proportional to the total fishing effort (n):

$$F = pn \qquad (4)$$

and that the catch per unit of effort is equivalent to the stock abundance (N). However, according to Low (1975), the catchability coefficient (p) may vary annually in accordance with several external factors such as random haul variations, weather conditions, temporal and diel variations in the distribution of the shad run, behavior of the shad with respect to the gear, skill of the fisherman, distribution of the units of gear throughout the season, and alteration in the gear's fishing power. Regarding Fredin's analysis of stock abundance, all or some of the above variables could have resulted in fluctuations of the catchability coefficient (p) among years. For this reason, it is necessary to discuss each factor while considering the nature of the commercial fishery.

For the shad fishery, large variations in(p)among individual units of effort are not too serious, since any variation which may occur will be reduced when the data are combined. Annual changes in (p) due to weather conditions are considered random, and will also be reduced when the data are averaged throughout the entire season. Though the entire run does not enter the river simultaneously, annual deviations in (p) with respect to temporal and diel movements of the shad are probably inappreciable, because the shad migrate upriver in clusters which are assumed to be similar among years (Fredin, 1954). The avoidance capability of certain fish to the gear could affect the precision of (p) with time, but this factor is difficult to assess and is considered negligible for the purposes of this investigation. Annual changes in (p) due to the abilities of certain fishermen to select more productive fishing grounds are inoperative for the shad fishery, because the run proceeds upriver in a predictable pattern each spring. Consequently, the fishermen are not required to search for productive areas. Annual changes in (p) due to a non-random distribution of fishing effort are assumed to be small, since during the season the fishing intensity increases with corresponding increases in the numbers of shad entering the river. Perhaps the most important influence on the estimate of (p) with time is the abrupt alteration in fishing power of a unit of effort. For example, yearly modification in the mesh sizes of drift gill nets, the materials of which the nets are made, the manner in which they are fished, or the power and size of the fishing vessels could alter the gear's catch efficiency, and thus affect the estimate of (p). However, because commercial fishing for shad is conducted today in essentially the same manner as it was forty years ago, sudden changes in the gear's fishing power are not expected to occur.

From the above discussion, large variations in the estimates of(p)with time are not anticipated. An analysis concerning the variation in (p) for the years 1966-1977 is provided in a subsequent section of this report.

From 1965 through 1973, the size of shad populations entering the river has been estimated by Leggett (1976), and the size of those during the period 1974-1977 has been monitored by the Connecticut Department of Environmental Protection (Jones et al. 1976). For these studies, the spaghetti dart tag was employed instead of the Petersen disk. At the end of each season, the fishermen were given a one dollar reward for each tag returned to the Department.

Because it is suspected that certain fishermen chronically under-report their catch, Leggett (1976) developed a statistical technique based on Chi square to determine which fishermen reported reliable catch data and to calculate an annual adjusted catch. Further details concerning the mathematical aspects of this technique are presented in Leggett (1976, p. 198-199).

Utilizing the adjusted catches and the number of reported tags, annual population estimates for the years 1965-1977 were obtained by substituting these data into equation (1). The stock estimates, reported catches, adjusted catches and the percent difference between reported and adjusted catches are shown in Table 1. The validity of the adjusted catches in column 3, as determined by Chi square analysis, is dependent upon the following assumptions: 1) the vulnerability of tagged fish to the nets of all fishermen was similar; 2) each fisherman returned all of his tags; and 3) most fishermen not only furnished all tags but also reported their true catch.

In these studies, the first assumption appears to have been satisfied, though variations in mesh size of the gill nets employed by certain fishermen could have resulted in some differential catchability of tagged fish. It can only be assumed that condition 2 has been fulfilled, since it is not known whether the one dollar reward provided adequate incentive to report all tags. During 1977, the State of Connecticut increased the reward to three dollars to further encourage tag reporting. The validity of the adjusted catches is primarily dependent upon the supposition that most commercial fishermen reported their true catch. However, if instead, most fishermen presented erroneous catch data, then the adjusted catches derived using Chi square would be in error. The above discussion certainly suggests that the validity of the Chi square analysis is predicated on tenuous assumptions. As a result, the adjusted catches should be viewed with caution.

The stock estimates, (1935-1951) as derived by Fredin were critically examined by Leggett (1976). He reasoned that the Petersen disk tag, employed during Fredin's 1951 tagging study, may have enhanced the vulnerability of tagged fish to the commercial gear resulting in too many recaptures. Thus, considering equation 3, the catchability coefficient (p) would have been too high, and the population estimates (N_x) too low. In addition, Fredin assumed that the annual catch reports submitted by the fishermen were entirely reliable. Though conclusive evidence to the contrary does not exist, it is suspected that certain fishermen chronically under-report their annual catch either because they failed to maintain adequate records, or because they were unwilling to claim their entire catch for tax purposes. This bias in the reported catches (C_x) would have made Fredin's stock estimates even lower.

Due to the possible errors associated with Fredin's stock estimates (1935-1951), Leggett (1976) attempted to recompute the shad runs for that period as well as those from 1952 through 1964. For this analysis, he used Fredin's catch and effort data for the period, 1935-1951; but for the 1952 through 1964 period, catch data were obtained from annual catch reports submitted by the fishermen (Connecticut Department of Environmental Protection, unpublished data), and annual effort (SFU) was determined by multiplying the number of nets registered with the State by 26 days - the average number of days fished, during the period 1948-1951 (Fredin, 1954). It was unnecessary to adjust the effort (SFU) for the period 1952-1964 according to gear types, since pound nets and haul seines were seldom used after 1951.

From 1965 through 1973, fishing effort (SFU) was determined annually by multiplying the number of nets registered with the state by 26 days. However, nets from fishermen who provided no catch reports but who returned several tags were excluded from these estimates of effort. This tactic was employed because Leggett reasoned that the state of Connecticut failed to enforce the reporting law prior to 1973.

After estimating the shad run, escapement, and effective fishing effort for the years 1965-1973, an estimate of the catchability coefficient (p) for each year was computed using equation (2). The best estimate of the true catchability coefficient is the mean estimate of ($\bar{p}$) for the nine year period. Thus Leggett

Table 1. Population estimates, reported commercial catches, adjusted commercial catches, and percent difference between reported and adjusted catches, 1965 - 1977.

	(1)	(2)	(3)	(4)
Year	Population[1/] estimate	Reported[2/] commercial catch	Adusted[3/] commercial catch	Percent[4/] difference between reported and adjusted catch
1965	1,470,000	84,426	173,103	105.0
1966	367,000	67,422	80,853	19.9
1967	368,000	67,695	75,869	12.0
1968	280,000	61.092	58,173	-5.0
1969	333,000	49,772	68,767	38.2
1970	419,000	48,484	71,367	47.2
1971	428,000	48,772	74,718	53.2
1972	275,000	48,968	51,197	4.6
1973	332,000	60,665	68,524	12.9
1974	372,000	55,910	61,509	10.0
1975	504,000	66,009	75,600	14.5
1976	740,000	90,807	107,761	18.7
1977	323,000	74,810	72,425	-3.2

1/ Data from 1965 through 1973 from Leggett (1976, Table 128, p. 206), and those from 1974 through 1977 are from Jones <u>et</u> <u>al</u>. (1976).

2/, 3/ Data from 1965 through 1973 from Leggett (1976, Table 119, p. 198-199), and those from 1974 through 1977 are from Jones et al. (1976).

4/ Rounded to the nearest 0.1%.

Table 2. Reported catch, adjusted catch, percent difference between reported and adjusted catch, fishing effort (SFU), and population estimate for each year, 1935 - 1973 as determined by Leggett (1976).

	(1)	(2)	(3)	(4)	(5)
Year	Reported commercial catch[1/]	Adjusted commercial catch[2/]	Percent difference between reported and adjusted catch	Fishing effort[3/]	Population estimates[4/]
1935	124,263	200,375	61.2	1,617	739,000
1936	106,459	166,975	56.8	1,504	704,000
1937	115,246	183,459	59.2	1,730	686,000
1938	125,356	202,425	61.5	1,918	693,000
1939	110,572	174,691	58.0	1,767	641,000
1940	95,703	141,410	47.8	1,265	694,000
1941	125,160	195,014	55.8	1,231	981,000
1942	110,520	182,662	65.3	1,298	877,000
1943	161,313	266,210	65.0	1,845	942,000
1944	214,086	364,901	70.4	2,554	990,000
1945	222,337	374,136	68.3	3,764	760,000
1946	301,556	529,657	75.6	5,309	861,000
1947	220,356	410,825	86.4	5,140	681,000
1948	175,250	299,745	71.0	4,118	573,000
1949	132,365	212,254	60.4	3,692	437,000
1950	77,853	111,879	43.7	2,749	287,000
1951	100,442	156,672	56.0	2,589	420,000
1952	136,402	223,148	63.6	2,808	714,000
1953	116,177	185,206	59.4	3,146	428,000
1954	83,828	124,519	48.5	2,418	353,000
1955	59,841	79,520	32.9	2,158	247,000
1956	55,285	70,973	28.4	1,716	267,000
1957	81,812	120,737	47.6	1,482	516,000
1958	128,381	208,101	62.1	2,002	688,000

continued

Table 2. continued

	(1)	(2)	(3)	(4)	(5)
Year	Reported[1] commercial catch	Adjusted[2] commercial catch	Percent difference between reported and adjusted catch	Fishing[3] effort	Population[4] estimates
1959	110,264	174,113	57.9	1,742	647,000
1960	115,971	184,825	59.4	1,768	678,000
1961	125,686	203,945	61.5	1,950	686,000
1962	121,206	194,640	60.6	2,054	630,000
1963	79,873	117,100	46.6	1,872	409,000
1964	75,597	109,078	44.3	1,612	433,000
1965	84,426	173,103	105.0	1,222	1,470,000
1966	67,422	80,853	19.9	1,040	367,000
1967	67,695	75,869	12.1	1,118	368,000
1968	61,092	58,173	-4.8	1,040	280,000
1969	49,772	68,767	38.2	1,092	333,000
1970	48,484	71,367	47.2	1,222	419,000
1971	48,772	74,718	53.2	1,274	428,000
1972	48,968	51,197	4.6	1,248	275,000
1973	60,665	68,524	12.9	1,404	332,000

1/ Reported catches, 1935 - 1939 were taken from Fredin (1954, Table 6, p. 255) and those thereafter (1940 - 1973) were obtained from the Connecticut Department of Environmental Protection, unpublished data.

2/ Adjusted catches, 1935 - 1964 were from Leggett (1976, Table 125, p. 205) and those thereafter were from Leggett (1976 Table 119, p. 198-199).

3/ Estimates of fishing effort (SFU), 1935 - 1951 were from Fredin (1954, Table 6, p.255), and those thereafter were from Leggett (1976, Tables 123 and 125, p. 203 and 205).

4/ Population estimates, 1935 - 1964 were from Leggett (1976, Table 125, p. 205) and those thereafter were from Leggett (1976, Table 124, p. 204).

(1976) reported an average catchability coefficient ($\bar{p}$) of 0.000180.

From his calculated $\bar{p}$ value, Leggett concluded that 0.018 percent of the shad run is removed after utilizing one SFU. In addition Leggett's estimated catchability coefficient (0.000180) was markedly lower than that (0.000325) derived by Fredin (1954). This tended to strengthen his earlier contention that in Fredin's 1951 study, the Petersen disk tag had increased the susceptibility of tagged fish to the gear, resulting in a catchability coefficient (p) which was too high and stock estimates which were too low.

According to Column 3, Table 1, of this report the adjusted catch for the 1965 shad run was 105% greater than the reported catch. From this observation, Leggett postulated that under-reporting increased with increasing size of the reported catch. Accordingly, he derived a technique for adjusting upward all of the historical catch data by using a linear regression based upon the reported (Column 2, Table 1) and adjusted catches (Column 3, Table 1) for the years 1965-1973 as follows:

$$Y_x = -32742 + 1.876 X_x \qquad (5)$$

where Y_x = adjusted catch in year x

X_x = reported catch in year x

The adjusted catches (column 2, Table 2) for the years, 1935-1964, were obtained by substituting the reported catches (Column 1, Table 2) for that period into equation (5). Given the adjusted catches (Y_x) and fishing effort (SFU) for the period 1935-1964 as well as the average $\bar{q}$ ($\bar{q} = 1-\bar{p}$), Leggett recomputed the size of the historical shad runs (Column 5, Table 2) using equation (3). It should be noted that many of the reported catches (Column 1) between 1935-1955 were adjusted by 40 to 80 percent (Column 3) above their original value. These stock estimates were used as the basis for Leggett's analysis on stock-recruitment.

Without detailed criticism of the generally fine work by Leggett (1976), both his 1965 population estimate and his adjusted catch appear to be overestimated and are in need of revision. In addition, Leggett's adjusted catches for the historical data (1935-1964) are no longer valid if the 1965 data are excluded, since the relationship between the reported and adjusted catches for the remaining years (1966-1977) do not support his earlier findings.

First, I shall discuss the problems with the 1965 population. According to Column 5, Table 2, Leggett's 1964 and 1965 populations, respectively, were estimated as 433,000 and 1,470,000 fish; an increase in one year of about one million individuals. For this to have occurred, at least 85 percent of the 1965 run would need to have been virgin recruits, because during 1964 some 323,922 fish survived the commercial fishery and escaped to the spawning area. This figure of 323,922 was computed using the following expression:

$$E_x = N_x - C_x \qquad (6)$$

where E_x = the number of fish escaping to the spawning ground in year x i.e. 323,922 in 1964

N_x = estimated size of the shad run in year x i.e. 433,000 in 1964 see Column 5, Table 2

C_x = adjusted commercial catch in year x i. e. 109,078 in 1964 see Column 2, Table 2.

But many of the 323,922 which escaped to the spawning ground in 1964 would have been lost to either the sport fishery upriver or to extraneous sources of mortality prior to 1965. For the purposes of this example, these additional sources of mortality will be collectively referred to as natural mortality. Between 1946 and 1947, Fredin (1954) estimated the annual rate of natural mortality to be 36 percent for age VI shad. Walburg (1961) reported an annual natural mortality rate of 58 percent for the years 1956-1959, whereas Leggett (1976) calculated an annual natural mortality rate of 52 percent from 1965 through 1973.

For the 1964 population, if we assume a natural mortality rate of 50 percent, approximately 162,000 of the 323,922 fish which escaped the commercial fishery would have returned in 1965 as repeat spawners. Assuming that the 1965 population of 1,470,000 fish was valid, repeat spawners should have constituted about 11 percent of the run during that year, i.e. $^{162{,}000}/_{1{,}470{,}000}$ = 11 percent. Yet Leggett's analysis of the spawning history (based on frequencies of age and spawning groups) of the 1965 population revealed that 52 percent (764,400 fish) of the 1,470,000 fish were repeat spawners (Leggett, 1976, Table 129, p 208). This figure of 764,000 represented nearly twice the entire 1964 population and thus could not have possibly occurred.

In addition, during 1965 many of the estimated 1,470,000 fish would have been expected to return in 1966 as repeat spawners, since such a dominant year class should have produced a large run in the following year. Substituting Leggett's 1965 population (1,470,000) and his adjusted catch (173,103) into equation 6, escapement during that year was estimated to be about 1,297,000 fish. Assuming an annual natural mortality rate of 50% between 1965 and 1966, then approximately 648,000 fish were expected to recur in 1966 as repeat spawners. But Leggett (1976) estimated the 1966 population as 367,000 fish, 194,510 (53%) of which were repeat spawners. These findings indicate that 1,102,490 fish perished from natural mortality prior to 1966. This figure of 1,102,490 was calculated using the following equation:

$$D_x = E_x - R_{x+1} \qquad (7)$$

where D_x = the number of fish lost to natural mortality in year x
i.e. 1,102,490 fish

E_x = escapement in year x
i.e. 1,297,000 fish during 1965

R_{x+1} = repeat spawners present during year x+1
i.e. 194,510 fish during 1966

Natural mortality of this dimension was equivalent to an instantaneous natural mortality rate (M) of 1.90 which is substantially greater than the average $\bar{M}$ (0.76; standard deviation, 0.28) for the period 1966 through 1973 (Leggett 1976, Table 135, p. 210).

The discrepancies in Leggett's data may have resulted from one or more of the following factors: the 1964 population and adjusted catch were underestimated, gross errors occurred in determining the numbers of repeat spawners in 1965, or the 1965 population and adjusted catch were overestimated. If the 1965 population was valid and the 1964 population was too low, then the true 1964 stock should have been well over a million fish to account for 764,400 repeat spawners present in 1965. This is because 109,078 fish had been taken by the commercial fishery in 1964 (Column 2, Table 2), while many others would have been lost to natural mortality previous to 1965. A 1964 population of well over a million fish is totally inconsistent with the adjusted catch and effort data for that year. In addition, an error of this extent in 1964 would cast doubt upon the accuracy of Leggett's previous population estimates (1935-1963).

Although errors in determining repeat spawners or from non-random sampling of fish for age determination could have induced a bias in the spawning history, such errors would need to have been extremely large to account for the observed discrepancies. Furthermore, these kinds of inconsistencies did not occur in data from subsequent years.

It is my contention that the discrepancies in Leggett's data were largely due to an overestimate of the 1965 population. Three factors may have contributed to a high 1965 population: tag-induced mortality, tag shedding, and the non-return of tags may have been inordinately high during the 1965 study. If these factors were instrumental in lowering the number of recaptures, then the 1965 population and adjusted catch would have been too high, since the accuracy of the Petersen equation and the Chi square test is very sensitive to errors in the number of recaptures. The above sources of bias are particularly relevant to the 1965 population for three reasons: first, the 1965 tagging study, being the first of its kind, was essentially a pilot survey. As a result, Leggett did not begin to examine the effects of either tag-induced mortality or tag shedding until 1966. Secondly, because the 1965 survey represents the first year of the study, certain fishermen may not have been informed as to the nature of the mark-recapture study. Consequently, some of the recaptured tags might not have been returned. Thirdly, during the spring of 1965 only 2,200 fish were tagged - the lowest number tagged throughout the entire period (1965-1977). I believe that the above evidence leads to the conclusion that Leggett's 1965 population and his adjusted catch are too high and are in need of further revision.

As previously stated, Leggett (1976) developed a linear regression model based on the reported and adjusted catches from 1965-1973 in an effort to estimate under-reporting for the historical data (1935-1964). The validity of this model depends upon Leggett's hypothesis that under-reporting increased with increases in the reported catch. His contention was strengthened by the 1965 data, since during that year the adjusted catch was 105% greater than the reported catch (Column 4, Table 1). The reasoning behind this hypothesis appears sound, because during particularly successful years certain fishermen would be more likely to declare a smaller portion of their catch to avoid higher income taxes. However, Leggett's postulate was not substantiated by the data from 1966 through

1977 (Column 4, Table 1). Excluding the 1965 data, the results of Chi square analysis suggests that the opposite hypothesis concerning under-reporting is true, since the greatest percent increase in the adjusted catches was manifested during 1969 - 1971 when the lowest reported catches were observed. Moreover, using linear regression analysis, there was no significant correlation between reported catches (Column 2, Table 1), and the percent difference of reported and adjusted catches (Column 4, Table 1), 1966 - 1977, ($t = 1.54$, d. f. = 10, $p < 0.10$). In fact, the correlation coefficient (r) was negative (-0.438), implying that an inverse relationship was more appropriate. The available data from 1966 through 1977 shows that Leggett's hypothesis concerning under-reporting is tenuous and that his stock estimates and adjusted catches for the years 1935 - 1965 need to be revised.

RECOMPUTATION OF STOCK ESTIMATES AND ADJUSTED CATCHES, 1940-1965

Because of the discrepancies in Leggett's 1965 population, and because his postulate regarding under-reporting was not supported by recent data (1966 - 1977), it was necessary to revise his stock estimates and his adjusted catches for the period, 1940 - 1965. My estimates of these data are based upon the reported catches and estimates of effective effort, 1940 - 1977 (Table 3). Since Fredin (1954) possessed incomplete information regarding the numbers of gill nets, haul seines, and pound nets in use from 1935 through 1939, he had no choice but to compute effort based upon data from adjacent years. For this reason, catch and effort data for the years 1935 - 1939 were excluded from my analysis.

In addition, my estimates of effort (SFU) from 1965 through 1969 were greater than those reported by Leggett (1976). This occurred because I estimated effort based upon all the nets registered during a given year, whereas Leggett excluded from his estimates of effort the nets from fishermen who reported no catch but who submitted tags. In order for Leggett's method to be consistent, the number of nets registered from previous years (1935 - 1964) would also have to be regulated accordingly. Furthermore, given just the tags, the Chi square analysis can provide an estimate of the catch, so there was no reason to exclude these fishermen from the effort estimate.

Fishing effort from 1975 through 1977 was estimated by multiplying the number of nets times the average number of days fished as determined from the fishermen's catch reports. This was necessary because from 1975 and onward the average days fishing had declined appreciably from 26 days.

Given the stock estimates, units of effort, and adjusted catches from 1966 through 1977, the average catchability coefficient ($\bar{p}$) and it's inverse ($\bar{q}$) were

Table 3. Reported catch, fishing effort, adjusted catch, and population estimates using both equation 3 and the mark-recapture technique for each year, 1940 - 1977.

	(1)	(2)	(3)	(4)	(5)
Year	Reported commercial catch	Fishing effort[1]	Adjusted commercial catch[2]	Population estimates using equation 3	Population estimates from mark-recapture
1940	95,703	1,265	108,336	546,000	
1941	125,160	1,231	141,681	731,000	
1942	110,520	1,298	125,109	616,000	
1943	161,313	1,845	182,606	662,000	
1944	214,086	2,554	242,345	672,000	
1945	222,337	3,764	251,685	522,000	
1946	301,556	5,309	341,361	564,000	
1947	220,356	5,140	249,443	420,000	
1948	175,250	4,118	198,383	386,000	
1949	132,363	3,692	149,837	315,000	
1950	77,853	2,749	88,130	231,000	
1951	100,442	2,589	113,700	312,000	
1952	136,402	2,808	154,407	398,000	
1953	116,177	3,146	131,512	311,000	
1954	83,828	2,418	94,893	275,000	
1955	59,841	2,158	67,740	215,000	
1956	55,285	1,716	62,583	241,000	
1957	81,812	1,482	92,611	405,000	
1958	128,381	2,002	145,327	492,000	
1959	110,264	1,742	124,819	475,000	
1960	115,971	1,768	131,279	493,000	
1961	125,686	1,950	142,277	492,000	
1962	121,206	2,054	137,205	454,000	
1963	79,873	1,872	90,416	324,000	
1964	75,597	1,612	85,576	348,000	

continued

Table 3. continued

	(1)	(2)	(3)	(4)	(5)
Year	Reported commercial catch	Fishing[1] effort	Adjusted[2] commercial catch	Population estimates using equation 3	Population estimates from mark-recapture
1965	84,426	1,560	95,570	400,000	
1966	67,422	1,326	80,853*	391,000	367,000
1967	67,695	1,326	75,869*	366,000	368,000
1968	61,092	1,300	58,173*	286,000	280,000
1969	49,772	1,144	68,767*	379,000	333,000
1970	48,484	1,144	71,367*	394,000	419,000
1971	48,772	1,092	74,718*	430,000	428,000
1972	48,968	1,222	51,197*	266,000	275,000
1973	60,665	1,378	68,524*	320,000	332,000
1974	55,910	1,196	61,509*	326,000	372,000
1975	66,009	1,020	75,600*	463,000	504,000
1976	90,807	1,070	107,761*	631,000	740,000
1977	74,810	1,176	72,425*	383,000	323,000

1/ Estimates of fishing effort, 1940 - 1951 were taken from Fredin (1954, Table 6, p. 255); those from 1952 - 1974 were determined by multiplying the number of nets registered with the state times 26 days; and effort from 1975 - 1977 was estimated by multiplying the number of nets registered times the average days fishing as determined from the fishermen's catch reports.

* Adjusted catches 1966 - 1977 were determined using Chi square analysis.

2/ Reported catch (column 1) times 1.132

Table 4. Estimates of the catchability[1/] coefficient (p) and it's inverse (q) for each year, 1966 - 1977 as well as the mean $\bar{p}$ and $\bar{q}$ using equation 2.

Year	(q) Value	(p) Value
1966	0.999812	0.000188
1967	0.999826	0.000174
1968	0.999821	0.000179
1969	0.999800	0.000200
1970	0.999837	0.000163
1971	0.999824	0.000176
1972	0.999830	0.000170
1973	0.999832	0.000168
1974	0.999849	0.000151
1975	0.999841	0.000159
1976	0.999853	0.000147
1977	0.999776	0.000224
Mean	0.999825	0.000175
Standard deviation	0.000021	0.000021

[1/] $q^nN = E$

where $q = (1-p)$

p = catchability coefficient (constant)

N = population size (Column 1, Table 1)

E = escapement = population size (N) - adjusted commercial catch (C)

Thus: $q = \sqrt[n]{E/N}$

calculated using equation (2) (see Table 4). My calculations reveal an average catchability coefficient ($\bar{p}$) of 0.000175 and it's inverse ($\bar{q}$) of 0.999825; the $\bar{p}$ value suggested that 0.0175 percent of the annual shad run is removed after utilizing one SFU such that F = 0.000175 n. My $\bar{p}$ and $\bar{q}$ values were slightly smaller than those ($\bar{p}$ = 0.000180; $\bar{q}$ = 0.999820) developed by Leggett (1976). In this investigation, the coefficient of variation (CV) of $\bar{p}$ is 12 percent indicating that the estimate of (p) and (q) for each of the twelve years is a fairly consistent value, and that the standard fishing unit day (SFU) appears to be a precise measurement of fishing effort.

Although the Chi square technique employed by Leggett (1976) is, at least, a consistent method for determining an adjusted catch, the problem of assessing the reliability of historical catch data remains unresolved. In this report, two conditions regarding the reliability of reported catches are assumed to be valid: 1) that certain fishermen under-report their catch for a variety of reasons, some of which have been previously stated; and 2) that the amplitude of under-reporting is essentially constant from one year to the next. After considering these conditions, the amount of under-reporting was estimated by determining the average percent difference between reported and adjusted catches for the years 1966 - 1967, and 1972 - 1976 (Column 4, Table 1). Data for the remaining years (1968 - 1971, and 1977) were excluded from this analysis for the following reasons: the Chi square test indicates that during 1968; commercial fishermen over-reported their catch by 5.0 percent (Column 4, Table 1), but in 1969 they appeared to under-report their catch by about 38.2 percent, and during 1970 and 1971, the analysis shows that under-reporting occurred at a rate of 47.2 percent and 53.2 percent, respectively. In 1977, Chi square indicated that the fishermen once again over-reported by 3.2 percent. These data do not seem

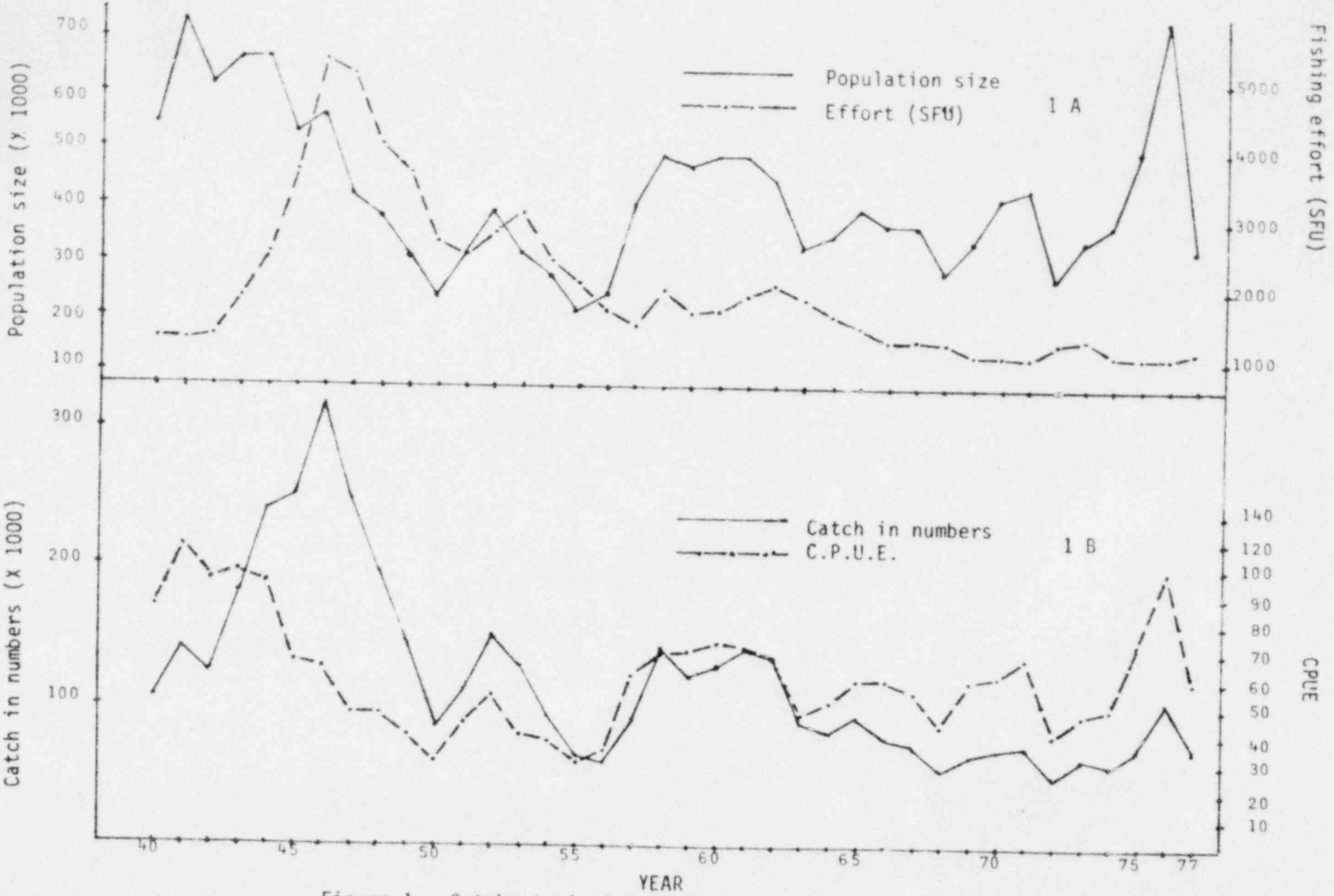

Figure 1. Catch statistics from the commercial shad fishery, 1940 - 1977:

A) Relationship between population size and fishing effort

B) Relationship between catch in numbers and CPUE

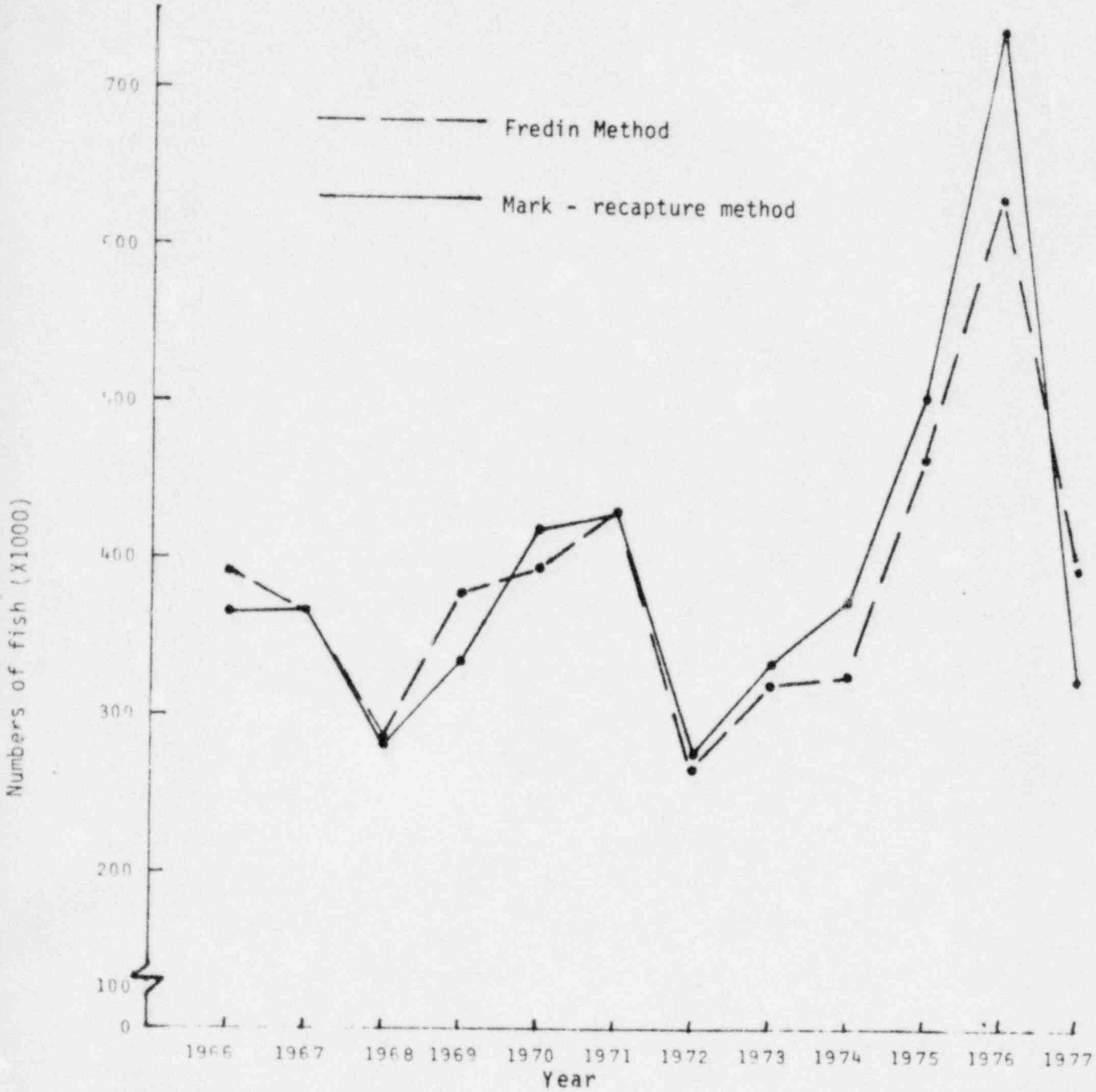

Figure 2. Population estimates as determined by the mark - recapture method compared to those developed by the Fredin method, 1966 - 1977.

to follow a logical pattern, for it is expected that certain fishermen would under-report a similar portion of their catch each year. For this reason the estimates from 1968 through 1971 and from 1977 are omitted from this analysis.

Based on the data for the periods 1966 - 1967 and 1972 - 1976, the average proportion of under-reporting amounted to 13.2 percent; all the reported catches from 1940 through 1965 were then increased by 13.2 percent above their original value to correct for under-reporting (Column 3, Table 3). It is important to note that the average percent of under-reporting based on all the data (1966 - 1977) is 18.6 percent, so that differences between the adjusted catches using either 13.2 or 18.6 percent are relatively small.

By substituting the adjusted catches, units of effort (SFU), and the mean $\bar{q}$ into equation 3, the size of the annual shad run was computed from 1940 through 1965 (Column 4, Table 3, Figure 1A). For the period 1966 - 1977, Figure 2 graphically illustrates the close agreement between stock estimates derived by equation (3) and those calculated by the mark-recapture method. These similarities are largely due to the low variance of the mean catchability coefficient ($\bar{p}$) observed throughout the 12 year period.

Another feature of interest respecting these data (Column 4, Table 3, Figure 1A) is that the amplitude and variation in the size of historical populations compare well with those from recent years (1966 - 1977). In addition, my estimate of the 1965 run is 400,000 individuals (Column 4, Table 3) as compared to Leggett's 1,470,000 fish. The revised 1965 population estimate is now consistent with the size of the 1964 population and with the proportion of repeat spawners present during 1965. For example, the 1964 run was estimated to be 348,000 fish (Column 4, Table 3). Because the commercial fishery had taken 85,576 fish (Column 3, Table3), escapement during 1964 was computed as 262,424 fish. As previously mentioned, Leggett (1976) reported that 52 percent of the 1965 stock were repeat spawners.

Thus, 208,000 fish were repeat spawners during 1965 i. e. 0.52 x 400,000 = 208,000 fish. Given an escapement of 262,424 fish during 1964, and 208,000 repeat spawners during 1965, a total of 54,424 fish were lost to natural mortality between years using equation (7).

From 1940 through 1977, the relationship between the size of the shad runs and changes in fishing effort (SFU) may be examined using Figure 1A. Figure 1B, shows the association between the catch in numbers and the catch per unit of effort (CPUE) for the same period. For the period 1940 - 1942, the main features of these data are the stability in fishing effort and the high CPUE. After the United States had entered World War II, beef rationing was imposed resulting in a greater demand for fish. Consequently, fishing effort rose from 1,298 SFU in 1942 to 1,845 SFU in 1943. Although CPUE began to dwindle after 1941, it still remained at a high level until 1945.

During 1944, fishing effort increased to 2,554 SFU, presumably because former fishermen had begun to return from military service, and because new fishermen had entered the fishery as a result of the fishing success experienced during the previous four years. In 1945, the fishery continued to expand causing a tremendous surge in landings which climaxed in 1946 by a record catch of 341,361 fish. Though the landings between 1944 and 1946 were high, CPUE started to diminish sharply. During the period 1940 through 1946, the prosperity of the fishery was largely dependent upon the successive entry into the fishery of at least two dominant year classes. However, conditions in the fishery changed rapidly thereafter. Between 1947 and 1950, the size of the shad runs began to noticeably decline due to recruitment of weak year classes into the fishery. Yet during this period the commercial fishery continued to operate at a high level of activity even though CPUE had declined. By 1956, yield in numbers had deteriorated to 62,583 fish.

Owing to the demonstrable reduction in fishing success evidenced from 1947 through 1956, fishing effort dropped from 2,158 SFU in 1955 to 1,716 SFU in 1956; and for the next nine years (1957 - 1965) it varied between 1,482 and 2,054 SFU. As a result, both CPUE and the size of the shad runs began to increase suggesting that the shad population was recovering from intense exploitation. From 1966 through 1975, fishing effort decreased even further and stabilized between 1,020 and 1,378 SFU. During this period, commercial landings deviated within narrow limits whereas CPUE varied widely; but CPUE was not to reach the high levels observed from 1940 through 1944 until 1976. A dominant year class entered the fishery in 1976 and both the catch and CPUE increased accordingly. Recruitment in 1977 was relatively low and fishing effort rose slightly but catch and CPUE diminished.

Assuming that the historical population estimates are valid on a relative basis, the observed decline of CPUE with corresponding increases in fishing effort during the late 1940's showed that overfishing was at least partially responsible for the decline in the shad population. For example, during the period 1943 - 1946, both fishing effort and catch increased dramatically; but CPUE and the shad population itself declined (Figures 1A and 1B). The rapid drop in the latter statistics was expected, for the fishery quickly exhausted the population of older, slower-growing fish that comprised the previously underfished stock. However, the CPUE could only have been kept from decreasing further, if the reproductive capacity of the stock had remained unaffected by the exploitation of adult females. Under intense fishing, such as that which occurred during the mid 1940's, annual removal of adult females may have been sufficiently great as to offset the annual replacement by virgin recruits four or five years thereafter, resulting in the partial collapse of the fishery.

This argument is further strengthened by what occurred in the fishery some years later. During 1957, following a decline in fishing effort, the shad population increased to a level comparable to those from the late 1940's, demonstrating that the shad population possesses the capacity for recovery.

In summary, the observed changes in the shad population with corresponding deviations in fishing effort have demonstrated that the commercial fishery exerted an immediate influence on the shad stocks. In addition, these data suggested further that the exploitation of adult females during the 1940's was sufficiently great as to noticeably reduce recruitment during later years. I recognize that the question of recruitment overfishing is still a controversial issue among fishery scientists, and the alternative argument can be made that the decline of the shad stocks during the period 1949 - 1956 was due to natural variations in recruitment. Nevertheless, the changes observed in such well-studied populations as the Downs herring, Clupea harengus (Cushing, 1968), the Arcto-Norwegian cod, Gadus morhua (Garrod, 1967) and the Pacific sardine, Sardinops caerulea, (Murphy, 1966) with variations in fishing effort offer evidence that exploitation by man can exert a real influence upon the size of a fish population.

The ability to successfully manage the shad in the Connecticut River can only be attained when the effect of fishing, and the biological parameters associated with the population are more clearly understood. Consequently, to comprehend these relationships, the underlying theory relating mortality, growth, and recruitment to yield is thoroughly explored in the following sections of this report.

AGE DETERMINATION

The ability to determine the age composition of the shad population is important for two reasons. First, each year's run is composed of fish from a number of year classes, and knowledge of the annual age structure is important to extrapolate recruitment to a particular level of escapement from past years. Second, annual estimates of the age structure in conjunction with stock estimates and length-weight measurements can provide information regarding the spawning history, the parameters of growth, natural mortality, fishing mortality and recruitment. As previously mentioned, these parameters are essential components in the proposed yield model.

From 1965 - 1977, the age structure of the shad run has been computed annually using scales from both the commercial and sport fisheries. The procedures employed to collect and age the scales were as follows: 12 scales were removed from the left side of each fish at a point located midcenter between the anterior edge of the dorsal fin and the lateral line. These scales were then placed in coin envelopes. Each fish was sexed, measured (fork length) to the nearest centimeter, and weighed to the nearest gram. Age was ascertained by counting annuli on the scales using the technique developed for shad by Cating (1953) and validated by Judy (1961). For each fish aged, the spawning history was also discerned by scale analysis using the following criterion: repeat spawners were noted by the presence of one or more prominent spawning scars near the periphery of the scale, whereas virgin recruits were determined by the absence of spawning scars. The ability to distinguish between virgin and repeat spawners would later aid in the determination of recruitment and mortality.

Age composition and spawning history by sex and year class are presented for the population during the years 1965 - 1973 by Leggett (1976, Tables 126 and 129, p. 205 and p. 208). However, information relating to the average length and weight by age group was not provided in his analysis. Since 1974, the Connecticut DEP has collected these data, on which I base my analysis of growth rates.

For the American shad, scales appeared to provide a reasonably reliable estimate of age, although age determination using scales is generally a difficult task. Errors in age determination using scales may occur due to the following factors: 1) inability to detect the first annulus (which lies close to the periphery of the freshwater mark), resulting in underestimation of age; 2) failure to distinguish between checks which are accessory and those which are true annuli, resulting usually in overestimation of age; and 3) failure to discern one or more year marks because of regeneration at the focus and/or because of erosion to the scale edge, resulting in a totally unreliable estimate of age. Errors of type 1 are eliminated by counting the freshwater mark as the first annulus. Though errors of type 2 may cause systematic bias in age determination, they can usually be averted with practice, since false annuli are usually less distinct than true year marks. Errors of type 3 can be very serious, because they may be partly random and partly systematic in nature. As a consequence, samples containing regenerated or eroded scales were useless for age determination, and thus were eliminated from further analysis. About 20 percent of the scales examined from 1974 - 1977 were undecipherable.

To circumvent the problem of unreliable scale samples, and to ensure a sufficient sample size, scale samples taken from the commercial fishery were partitioned by sex and stratified into one centimeter size groups. The samples from the sport fishery were subdivided in the same manner. The length-frequency ogive of all size groups approximated a bell-shaped (normal) distribution.

Table 5. Age composition and spawning history of male shad as determined by scales from the sport fishery Enfield, 1974 - 1977.

Age Group	III	IV	V	VI	VII	VIII
Year 1974						
Number of fish (142)	22	38	53	26	2	1
% Age	15.5	26.8	37.3	18.3	1.4	0.7
% Repeat spawners	0.0	29.0	58.5	80.8	100.0	100.0
% Virgin	100.0	71.0	41.5	19.2	0.0	0.0
Year 1975 [1/]						
Number of fish	-	-	-	-	-	-
% Age	19.7	42.3	27.6	9.9	0.5	-
% Repeat spawners	-	-	-	-	-	-
% Virgin	-	-	-	-	-	-
Year 1976						
Number of fish (27)	4	14	7	2	-	-
% Age	14.8	51.9	25.9	7.4	-	-
% Repeat spawners	0.0	9.1	28.6	100.0	-	-
% Virgin	100.0	90.9	71.4	0.0	-	-
Year 1977						
Number of fish (52)	15	25	10	2	-	-
% Age	28.8	48.1	19.2	3.9	-	-
% Repeat spawners	0.0	4.0	60.0	100.0	-	-
% Virgin	100.0	96.0	40.0	0.0	-	-

[1/] Enfield scales not taken; age distribution during 1975 was estimated by averaging the age compositions during 1974, 1976 and 1977.

able 6. Age composition and spawning history of female shad as determined by scales from the sport fishery Enfield, 1974 - 1977.

Age Group	IV	V	VI	VII	VIII
Year 1974					
Number of fish (261)	46	146	44	19	6
% Age	17.6	55.9	16.9	7.3	2.3
% Repeat spawners	0.0	24.7	70.4	100.0	100.0
% Virgin	100.0	75.3	29.6	0.0	0.0
Year 1975 1/					
Number of fish					
% Age	19.4	64.8	12.2	2.8	0.8
% Repeat spawners					
% Virgin					
Year 1976					
Number of fish (82)	13	60	8	1	-
% Age	15.9	73.2	9.7	1.2	-
% Repeat spawners	0.0	13.8	62.5	100.0	-
% Virgin	100.0	86.2	37.5	0.0	-
Year 1977					
Number of fish (81)	20	53	8	-	-
% Age	24.7	65.4	9.9	-	-
% Repeat $pawners	0.0	15.0	50.0	-	-
% Virgin	100.0	85.0	50.0	-	-

/ Enfield scales not taken; age distribution during 1975 was estimated by averaging the age compositions during 1974, 1976 and 1977.

Approximately 50 percent of the scale samples for each size interval were randomly subsampled according to the technique derived by Ketchen (1950) and analyzed for age and spawning history. At both ends of the length-frequency distribution, when the number of scale samples was less than 8, age determinations were made for all samples. In this case, the method of sampling deviated from a true stratified sample since above and below certain length-groups the numbers of age determinations were greater than the 50 percent level chosen for stratification. However, this modification of the technique ensured that the larger and smaller size groups would be adequately represented in the sub-sample while age determination of unnecessarily large numbers of scale samples at the peak of the length frequency distribution would be avoided. During the subsampling process, scale samples considered to be undecipherable were placed back in their respective size groups and other samples were randomly chosen in their place. After estimating the age from all subsamples, the results were then extrapolated to all the samples that constituted the length frequency distribution.

The theoretical and statistical validity of Ketchen's stratified sampling method was reviewed by Gulland (1955, 1962) and by Pope (1956). Pinhorn and Fleming (1965) aged cod otoliths using Ketchen's method and compared the results to those from random sampling. They concluded that the age distribution and average length by age group were similar for both types of sampling, but that stratified sampling was far less time consuming.

From 1974 - 1977, the age distribution and spawning history by sex are shown in Tables 5 - 8 for fish taken in the commercial and sport fisheries. The age distributions by sex from the sport fishery samples (Tables 5 and 6) were similar to those reported by Nichols and Tagatz (1960, Table 7, p. 9). The average age composition revealed that most males were age III (19.7 percent), ble 7. Age composition and spawning history of <u>male shad</u> as determined by scales from the commercial fishery, 1974 - 1977.

Age Group	III	IV	V	VI	VII	VIII
Year 1974						
Number of fish (89)	7	32	33	15	2	-
% Age	7.9	36.0	37.0	16.9	2.2	-
% Repeat spawners	0.0	18.7	48.5	93.3	100.0	-
% Virgin	100.0	81.3	51.5	6.7	0.0	-
Year 1975						
Number of fish (211)	4	93	81	32	1	-
% Age	1.9	44.1	38.4	15.1	0.5	-
% Repeat spawners	0.0	11.8	50.6	93.8	100.0	-
% Virgin	100.0	88.2	49.4	6.2	0.0	-
Year 1976						
Number of fish (138)	4	36	88	10	-	-
% Age	2.9	26.1	63.8	7.2	-	-
% Repeat spawners	0.0	8.3	34.1	90.0	-	-
% Virgin	100.0	91.7	65.9	10.0	-	-
Year 1977						
Number of fish (101)	14	48	35	4	-	-
% Age	13.9	47.5	34.6	4.0	-	-
% Repeat spawners	0.0	25.0	45.7	100.0	-	-
% Virgin	100.0	75.0	54.3	0.0	-	-

Table 8. Age composition and spawning history of <u>female shad</u> as determined by scales from the commercial fishery, 1974 - 1977.

Age Group	IV	V	VI	VII	VIII
Year 1974					
Number of fish (270)	34	167	52	13	4
% Age	12.6	61.8	19.3	4.8	1.5
% Repeat spawners	0.0	11.4	76.9	100.0	100.0
% Virgin	100.0	88.6	23.1	0.0	0.0
Year 1975					
Number of fish (286)	54	193	37	2	-
% Age	18.9	67.4	13.0	0.7	-
% Repeat spawners	0.0	12.9	73.3	100.0	-
% Virgin	100.0	87.1	26.7	0.0	-
Year 1976					
Number of fish (390)	39	331	17	3	-
% Age	10.0	84.9	4.3	0.8	-
% Repeat spawners	0.0	12.4	64.7	100.0	-
% Virgin	100.0	87.6	35.3	0.0	-
Year 1977					
Number of fish (441)	64	320	55	2	-
% Age	14.5	72.6	12.5	0.4	-
% Repeat spawners	0.0	12.8	40.0	100.0	-
% Virgin	100.0	87.2	60.0	0.0	-

IV (42.3 percent), and V (27.5 percent), whereas the majority of females belonged to ages IV (19.4 percent), and V (64.8 percent). Neither age III females nor age II males were observed throughout the four year period.

The age composition for male shad from the commercial samples (Table 7) showed that 38.4 percent were age IV and 43.4 percent were age V. In the commercial samples, age III males only comprised 6.7 percent of those of those sampled as compared to 19.7 percent from the sport fishery samples. In contrast, most females were from age group V (71.7 percent), whereas age IV females comprised 14.0 percent of those sampled commercially (Table 8). The age distributions as determined from commercial samples for 1974 - 1977 could not be compared to those for 1965 - 1973 as derived by Leggett (1976), since he did not present the respective age distributions from the sport and commercial fisheries in separate tables.

To provide the best estimate of the true age structure, the age compositions from both fisheries were given equal weight and combined according to sex (Tables 9 and 10). This procedure was necessary because as mentioned earlier, the commercial fishery employs drift gill nets which are suspected to select for the longer and heavier females and for the older males of the population. In contrast, the sport fishery is believed to be less selective than the commercial fishery owing to the diversity of fishing strategies (i.e. shore fishing and boat fishing) and fishing tackle (e. g. variations in hook size - darts, spinners, spoons, etc.) employed by anglers.

For the fisheries combined, 1974 - 1977 (Tables 9 and 10), the age compositions by sex agreed well with those from the period 1965 - 1973 as reported by Leggett (1976, Table 126, p. 205). Moreover, the spawning data showed that males mature about one year earlier than do females, which agrees with previous studies (Nichols and Tagatz, 1960; Walburg, 1961, 1963; Leggett, 1969, 1976; and Foote, 1976). In this investigation,the proportion of repeat spawners of both sexes generally declined from 1974 - 1977 (Figure 3). This trend was not evident from the data

Table 9. Age composition and spawning history of male shad as determined by scales from the commercial and sport fishery combined, 1974 - 1977.

Age Group	III	IV	V	VI	VII	VIII
Year 1974						
% Age composition	11.7	31.4	37.1	17.6	1.8	0.4
% Repeat spawners	0.0	23.8	53.5	87.0	100.0	100.0
% Virgin	100.0	76.2	46.5	13.0	0.0	0.0
Year 1975						
% Age composition	10.8	43.2	33.0	12.5	0.5	-
% Repeat spawners*	0.0	11.8	50.6	93.8	100.0	-
% Virgin*	100.0	88.2	49.4	6.2	0.0	-
Year 1976						
% Age Composition	8.9	39.0	44.8	7.3	-	-
% Repeat spawners**	0.0	8.3	34.1	90.0	-	-
% Virgin **	100.0	91.7	65.9	10.0	-	-
Year 1977						
% Age composition	21.4	47.8	26.9	3.9	-	-
% Repeat spawners	0.0	14.5	52.8	100.0	-	-
% Virgin	100.0	85.5	47.2	0.0	-	-

* Spawning history during 1975 was determined from commercial scales only.

** Because only 27 scale samples were taken from the sport catch, spawning history during 1976 was determined from commercial scales.

Table 10. Age composition and spawning history of female shad as determined by scales from the commercial and sport fishery combined, 1974 - 1977.

Age Group	IV	V	VI	VII	VIII
Year 1974					
% Age composition	15.1	58.9	18.1	6.0	1.9
% Repeat spawners	0.0	18.0	73.6	100.0	100.0
% Virgin	100.0	82.0	26.4	0.0	0.0
Year 1975					
% Age composition	19.2	66.1	12.6	1.7	0.4
% Repeat spawners*	0.0	12.9	73.3	100.0	100.0
% Virgin*	100.0	87.1	26.7	0.0	0.0
Year 1976					
% Age composition	13.0	79.0	7.0	1.0	-
% Repeat spawners	0.0	13.1	63.6	100.0	-
% Virgin	100.0	86.9	36.4	0.0	-
Year 1977					
% Age composition	19.6	69.0	11.2	0.2	-
% Repeat spawners	0.0	13.9	45.0	100.0	-
% Virgin	100.0	86.1	55.0	0.0	-

* Spawning history during 1975 was determined by commercial scales only.

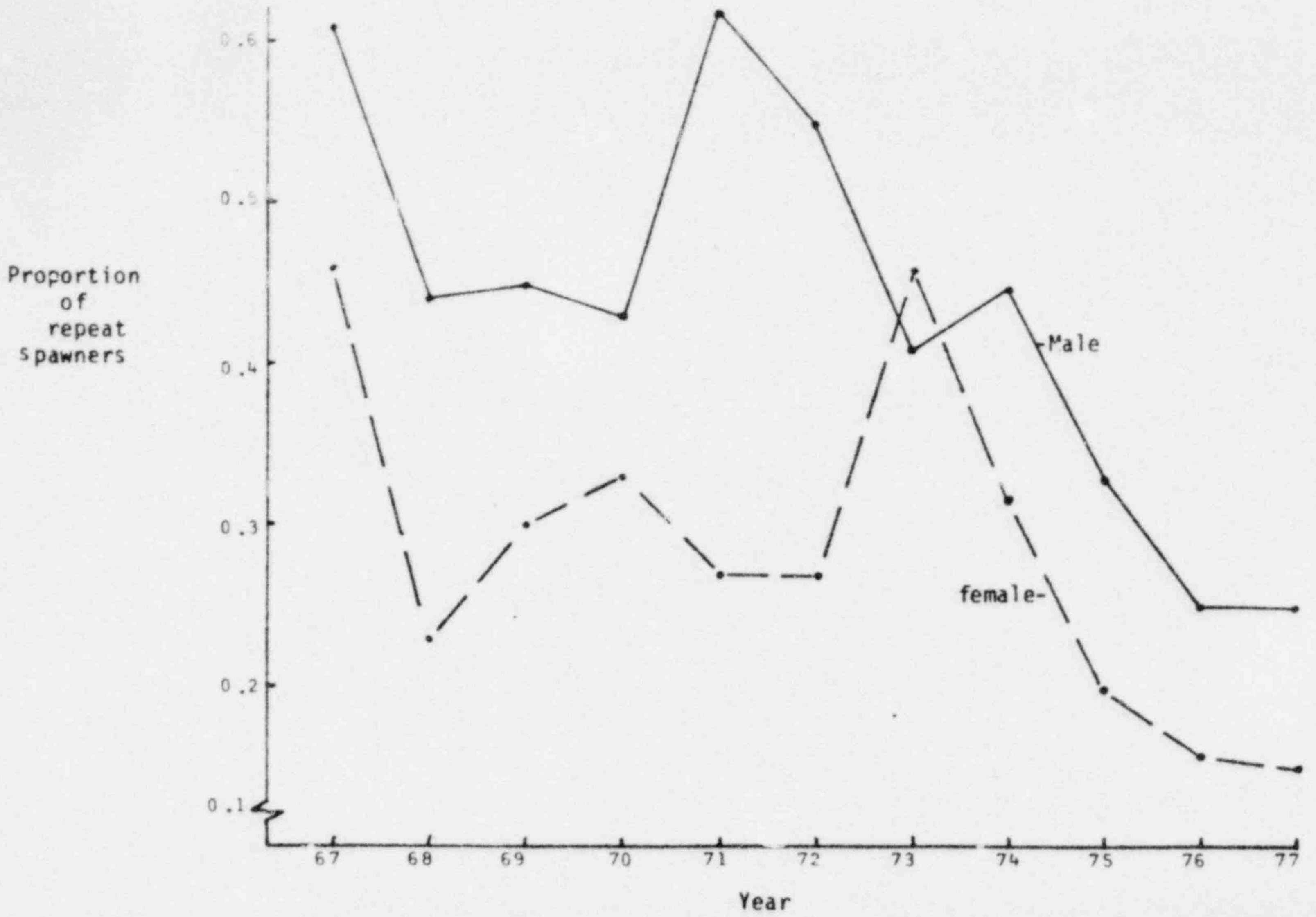

Figure 3. Proportion of repeat spawners by sex as determined from scale analysis, 1967 - 1977

collected during the previous nine years (1965 - 1973). Possible reasons for this recent decline in repeat spawners will be discussed in a subsequent section pertaining to mortality.

The average proportion of repeat spawners was greater for males (32.0 percent) than for females (20.6 percent) for the years 1974 - 1977. There has been a general lack of agreement among previous studies concerning the magnitude of repeat spawning among male and female shad in the Connecticut River. For example, after analyzing scale samples from the sport fishery, Nichols and Tagatz (1960) reported that during 1957 and 1958, repeat spawners comprised 13.6 and 15.3 percent, respectively, of the female and male fish examined. Leggett (1976) analyzed scales from both fisheries, 1965 - 1973, and found that repeat spawners averaged 53.2 percent for males and 35.1 percent for females. Walburg (1961) analyzed scale samples from the commercial catch, 1956 - 1959, and revealed that, on the average, 48.2 percent of those fish sampled were repeat spawners, whereas Foote (1976) studies the age structure of the shad from above the Holyoke Dam and found that repeat spawning occurred at a greater rate for females (15.5 percent) than for males (10.4 percent). The deviations in the proportion of repeat spawners recorded from previous studies are largely due to differences in gear selectivity between the commercial and sport fisheries, modification of the age structure from above Holyoke resulting from the commercial and sport fisheries, and variations in year class recruitment.

ESTIMATES OF GROWTH PARAMETERS

Because growth is one of the four principal parameters in an effective yield model, it should be represented in a form which is not only biologically sound but is also mathematically suitable. In general, fish grow rapidly in length during the larval and juvenile stages, but more slowly with maturation and much more slowly during old age. Yet fish grow in weight continuously, and during the period following sexual maturity they may gain weight rapidly. Any study of the effect of fishing upon the adult shad stock involves the maximization of gains in weight concurrent with loss of numbers due to fishing and natural causes. Moreover, growth in terms of length and weight is probably the easiest of the four parameters to measure, and can be adequately described for most fishes by a sigmoid curve as derived by von Bertalanffy (1938).

For the years 1974 - 1977, average fork lengths (cm) and average weights (kg) by age group and sex for the commercial and sport fisheries, respectively, are assembled in Tables 11 and 12. To correct for possible growth bias due to the selective retention of the faster-growing individuals by the gill net fishery, the length and weight data from both fisheries were weighed equally and combined (Tables 13 and 14). Since no differences in average length by age group were apparent among years, I combined the estimates from 1974 - 1977 and determined the average length by age and sex (Table 15). A comparison of length at age shows that females are always longer than males at a given age. Whether this relationship persists for sexually immature males (ages I and II) and females (ages I, II, and III) is not known since length-age data by sex are unavailable for immature shad. These findings for mature shad parrallel those from previous investigations in the Connecticut River (Nichols and Tagatz, 1960; Walburg and Nichols, 1967; Foote, 1976) as well as those from a study conducted in the

Table 11. Various statistics (mean, standard deviation, 95% fiducial limits)[1/] on both fork length (cm) and weight (kg) for each age group by sex from the commercial fishery, 1974 - 1977.

Year 1974

Males

Age group	III	IV	V	VI	VII	VIII
N(89)	7	32	33	15	2	-
Mean fork length (cm)	40.20	43.88	46.23	49.33	51.00	-
Standard deviation	1.30	1.22	1.19	0.970	1.41	-
95% fiducial limits	-	41.44-46.32	43.85-48.61	47.39-51.27	-	-
Mean weight (kg)	1.020	1.388	1.600	1.900	2.013	-
Standard deviation	0.179	0.167	0.217	0.255	-	-
95% fiducial limits	-	1.054-1.722	1.166-2.034	1.390-2.410	-	-

continued

Table 11. Continued

Year 1974

Females

Age Group	III	IV	V	VI	VII	VIII
N (270)	-	34	167	52	13	4
Mean fork length (cm)	-	44.86	49.04	51.93	53.51	56.10
Standard deviation	-	1.28	1.62	2.42	2.60	3.79
95% fiducial limits	-	42.30-47.42	45.80-52.28	47.09-56.77	48.31-58.71	-
Mean weight (kg)	-	1.663	2.081	2.533	2.881	3.078
Standard deviation	-	0.171	0.229	0.419	0.408	0.374
95% fiducial limits	-	1.321-2.005	1.623-2.539	1.695-3.371	2.065-3.697	-

continued

Table 11. Continued

Year 1975 Males

Age group	III	IV	V	VI	VII	VIII
N (211)	4	93	81	32	1	-
Mean fork length (cm)	38.50	42.88	46.48	49.43	53.00	-
Standard deviation	0.71	1.93	1.31	1.72	-	-
95% fiducial limits	-	39.02-46.74	43.86-49.10	45.99-52.87	-	-
Mean weight (kg)	1.050	1.321	1.691	1.839	2.355	-
Standard deviation	0.148	0.213	0.149	0.197	-	-
95% fiducial limits	-	0.895-1.747	1.393-1.989	1.445-2.233	-	-

Table 11. Continued

Year 1975 Females

Age group	III	IV	V	VI	VII	VIII
N (286)	-	54	193	37	2	-
Mean fork length (cm)	-	45.07	48.81	51.39	53.50	-
Standard deviation	-	1.83	1.88	2.22	0.71	-
95% fiducial limits	-	41.41-48.73	45.06-52.57	46.95-55.83	-	-
Mean weight (kg)	-	1.691	2.137	2.533	3.125	-
Standard deviation	-	0.230	0.278	0.399	0.119	-
95% fiducial limits	-	1.231-2.151	1.581-2.693	1.735-3.331	-	-

continued

Table 11 Continued

Year 1976

Males

Age group	III	IV	V	VI	VII	VIII
N (138)	4	36	88	10	-	-
Mean fork length (cm)	39.75	43.27	45.70	49.10	-	-
Standard deviation	1.258	1.710	1.78	1.29	-	-
95% fiducial limits	-	39.85-46.69	42.14-49.26	46.52-51.68	-	-
Mean weight (kg)	0.932	1.306	1.553	1.723	-	-
Standard deviation	0.089	0.185	0.120	0.160	-	-
95% fiducial limits	-	0.936-1.676	1.313-1.793	1.403-2.043	-	-

continued

Table 11 Continued

Year 1976

Age group	III	IV	V	VI	VII	VIII
N (390)	-	39	331	17	3	-
Mean fork length (cm)	-	45.40	48.59	52.56	54.67	-
Standard deviation	-	0.99	1.53	1.42	0.58	-
95% fiducial limits	-	43.42-47.38	45.53-51.65	49.72-55.40	-	-
Mean weight (kg)	-	1.775	2.007	2.528	2.933	-
Standard deviation	-	0.126	0.175	0.287	0.351	-
95% fiducial limits	-	1.523-2.027	1.667-2.357	1.954-3.102	-	-

Females

continued

Table 11 Continued

Year 1977 Males

Age group	III	IV	V	VI	VII	VIII
N (101)	14	48	35	4	-	-
Mean fork length (cm)	40.28	43.83	46.51	48.75	-	-
Standard deviation	1.38	1.37	1.28	1.18	-	-
95% fiducial limits	37.52-43.04	41.09-46.57	43.95-49.07	-	-	-
Mean weight (kg)	1.093	1.478	1.681	2.022	-	-
Standard deviation	0.126	0.241	0.220	0.320	-	-
95% fiducial limits	0.841-1.345	0.996-1.960	1.241-2.121	-	-	-

continued

Table 11 Continued

Year 1977 Females

Age group	III	IV	V	VI	VII	VIII
N (441)	-	64	320	55	2	-
Mean fork length (cm)	-	45.61	49.16	52.18	54.50	-
Standard deviation	-	0.92	1.63	1.63	0.71	-
95% fiducial limits	-	43.77-47.45	45.90-52.42	48.92-55.44	-	-
Mean weight (kg)	-	1.824	2.184	2.478	2.860	-
Standard deviation	-	0.138	0.194	0.243	0.057	-
95% fiducial limits	-	1.5 8-2.100	1.796-2.572	1.992-2.964	-	-

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[1] Fiducial limits not calculated for age groups with seven or fewer samples.

Table 12. Various statistics (mean, standard deviation, 95% fiducial limits)[1/] on both fork lengths (cm) and weight (kg) for each age group by sex from the sport fishery Enfield, 1974-1977.

Year 1974

Males

Age groups	III	IV	V	VI	VII	VIII
N (142)	22	38	53	26	2	1
Mean fork length (cm)	37.82	42.84	46.08	48.96	50.50	54.00
Standard deviation	1.33	1.50	1.35	1.27	0.71	-
95% fiducial limits*	35.16-40.48	39.84-45.84	43.38-48.78	46.42-51.50	-	-
Mean weight (kg)	0.731	1.114	1.359	1.586	1.900	2.423
Standard deviation	0.125	0.150	0.191	0.264	0.424	-
95% fiducial limits	0.481-.981	0.814-1.414	0.977-1.741	1.058-2.114	-	-

continued

Table 12 Continued

Year 1974 Females

Age groups	III	IV	V	VI	VII	VIII
N (261)	-	46	146	44	19	6
Mean fork length (cm)	-	45.46	49.18	52.70	54.81	56.50
Standard deviation	-	1.69	1.65	1.73	2.02	1.05
95% fiducial limits	-	42.08-48.84	45.88-52.48	49.24-56.16	50.77-58.85	-
Mean weight (kg)	-	1.556	1.966	2.427	2.854	3.050
Standard deviation	-	0.215	0.206	0.394	0.507	0.365
95% fiducial limits	-	1.126-1.986	1.554-2.378	1.639-3.215	1.840-3.868	2.320-3.780

Year 1975 No Enfield scales taken

continued

Table 12 Continued

Year 1976 Males

Age groups	III	IV	V	VI	VII	VIII
N (27)	4	14	7	2	-	-
Mean fork length (cm)	37.00	41.71	46.28	49.00	-	-
Standard deviation	0.82	1.33	1.60	0.0	-	-
95% fiducial limits	-	39.05-44.37	-	-	-	-
Mean weight (kg)	0.755	1.087	1.381	1.860	-	-
Standard deviation	0.039	0.146	0.185	0.170	-	-
95% fiducial limits	-	0.795-1.379	1.011-1.751	-	-	-

continued

Table 12 Continued

Year 1976 Females

Age groups	III	IV	V	VI	VII	VIII
N (82)	-	13	60	8	1	-
Mean fork length (cm)	-	44.00	47.74	50.28	54.00	-
Standard deviation	-	1.00	1.85	1.25	-	-
95% fiducial limits	-	42.00-46.00	44.04-51.44	47.78-52.78	-	-
Mean weight (kg)	-	1.423	1.825	1.943	2.768	-
Standard deviation	-	0.154	0.267	0.195	-	-
95% fiducial limits	-	1.115-1.731	1.291-2.359	1.553-2.333	-	-

continued

Table 12 Continued

Year 1977 Males

Age groups	III	IV	V	VI	VII	VIII
N (52)	15	25	10	2	-	-
Mean fork length (cm)	39.07	43.28	46.60	48.50	-	-
Standard deviation	1.03	1.49	1.71	0.71	-	-
95% fiducial limits	37.01-41.13	40.30-46.26	43.18-50.02	-	-	-
Mean weight (kg)	0.890	1.133	1.314	1.575	-	-
Standard deviation	0.119	0.138	0.135	0.092	-	-
95% fiducial limits	0.652-1.128	0.857-1.409	1.044-1.584	-	-	-

continued

Table 12 Continued

Year 1977 Females

Age groups	III	IV	V	VI	VII	VIII
N (81)	-	20	53	8	-	-
Mean fork length (cm)	-	44.85	48.85	51.38	-	-
Standard deviation	-	1.57	1.56	2.07	-	-
95% fiducial limits	-	41.71-47.99	45.73-51.97	47.24-55.52	-	-
Mean weight (kg)	-	1.431	1.938	2.258	-	-
Standard deviation	-	0.160	0.215	0.211	-	-
95% fiducial limits	-	1.111-1.751	1.508-2.368	1.836-2.680	-	-

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1/ Fiducial limits not calculated for age groups with seven or fewer samples.

Table 13. Average fork length (cm) at each age group by sex as determined for samples from both the commercial and sport fisheries combined, 1974 - 1977.

Males

Age group	III	IV	V	VI	VII	VIII
Year						
1974	39.01	43.36	46.16	49.15	50.75	54.00[1/]
1975[2/]	38.50	42.88	46.48	49.43	53.00[1/]	-
1976	38.38	42.49	45.99	49.05	-	-
1977	39.68	43.56	46.56	48.63	-	-
Mean	38.89	43.07	46.30	49.07	50.75	-
Standard deviation	0.59	0.48	0.27	0.33	-	-

Females

Age group	III	IV	V	VI	VII	VIII
1974	-	45.16	49.11	52.32	54.16	56.30
1975[2/]	-	45.07	48.81	51.39	53.50	-
1976	-	44.70	48.17	51.42	54.34	-
1977	-	45.23	49.01	51.78	54.50	-
Mean	-	45.04	48.78	51.73	54.12	56.30
Standard deviation	-	0.24	0.42	0.43	0.44	-

[1/] Only one sample available; it was not used to determine average length.

[2/] Only commercial samples used to determine average length for 1975.

Table 14. Average weight (kg) at each age group by sex as determined for samples from both the commercial and sport fisheries combined, 1974 - 1977.

Males

Age group	III	IV	V	VI	VII	VIII
Year						
1974	0.876	1.251	1.480	1.743	1.957	2.423[1/]
1975[2/]	1.050	1.321	1.691	1.839	2.355[1/]	-
1976	0.844	1.197	1.467	1.792	-	-
1977	0.992	1.306	1.498	1.799	-	-
Mean	0.941	1.269	1.534	1.793	1.957	-
Standard deviation	0.097	0.057	0.105	0.039	-	-

Females

Age group	III	IV	V	VI	VII	VIII
1974	-	1.610	2.024	2.480	2.868	3.064
1975[2/]	-	1.691	2.137	2.533	3.125	-
1976	-	1.599	1.916	2.236	2.851	-
1977	-	1.628	2.061	2.368	2.860	-
Mean	-	1.632	2.035	2.404	2.926	3.064
Standard deviation	-	0.041	0.092	0.132	0.133	-

[1/] Only one sample available ; it was not used to determine average weight.

[2/] Only commercial samples used to determine average weight for 1975.

Table 15. Average fork length (L_t) at age t and average fork length (L_{t+1}) of successive ages (t+1) for male and female shad, 1974 - 1977.

Males				Females			
Age t	L_t	Age t+1	L_{t+1}	Age t	L_t	Age t+1	L_{t+1}
III	38.89	IV	43.07	IV	45.04	V	48.78
IV	43.07	V	46.30	V	48.78	VI	51.73
V	46.30	VI	49.07	VI	51.73	VII	54.12
VI	49.07	VII	50.75	VII	54.12	VIII	56.30
VII	50.75			VIII	56.30		

Delaware River (Chittenden, 1975). Perhaps the main reason for length differences between males and females is that males reach sexual maturity at age III or IV whereas females achieve maturity mostly at age V. Therefore, during the years following sexual maturity, age III and IV males must divert some energy to produce sexual products at the expense of somatic growth in length.

According to Beverton and Holt (1957), the growth rate of a fish population is best represented by the von Bertalanffy growth equation, which has become widely accepted for use in growth studies during recent years. In this model growth in length with age is depicted by the expression:

$$L_t = L\infty \left[1 - e^{-K(t-t_o)}\right] \qquad (8)$$

where L_t = average length at age t (in years)

$L\infty$ = theoretical maximum length

K = exponential growth rate with respect to age

t_o = hypothetical age at zero length if the fish had always grown according to the model.

To obtain estimates of the above parameters, the Walford plot as described by Mr. Howard Russell (unpublished manuscript) was employed: for each sex, the average fork length at age (L_t) from Table 15 was regressed against the average fork length of the succeeding age (L_{t+1}) yielding the linear equation:

$$L_{t+1} = a+bl_t \qquad (9)$$

The parameters of the model ($L\infty$, K, t_o) were then estimated using the following expressions:

$$L\infty = a/(1-b) \qquad (10)$$

$$K = -\ln b \qquad (11)$$

and $$t_o = t+\frac{1}{K} \ln\left[\frac{L\infty - L_t}{L\infty}\right] \qquad (12)$$

Values of $L\infty$ as determined for each sex using the above equations are shown

Table 16. Calculated [1/] and observed average fork length (cm) by age and sex.

Males			Females		
(1) Age	(2) Obs. average length	(3) Calc. average length	(4) Age	(5) Obs. average length	(6) Calc. average length
II	-	33.20	II	-	35.29
III	38.89	38.76	III	-	40.68
IV	43.07	43.03	IV	45.04	45.12
V	46.30	46.33	V	48.78	48.81
VI	49.07	48.81	VI	51.73	51.79
VII	50.75	50.73	VII	54.12	54.28
VIII	-	52.21	VIII	56.30	56.32
IX	-	53.34	IX	-	58.01
X	-	54.20	X	-	59.40
XI	-	54.87	XI	-	60.54

[1/] Calculated average length by age group was computed using the von Bertalanffy growth model.

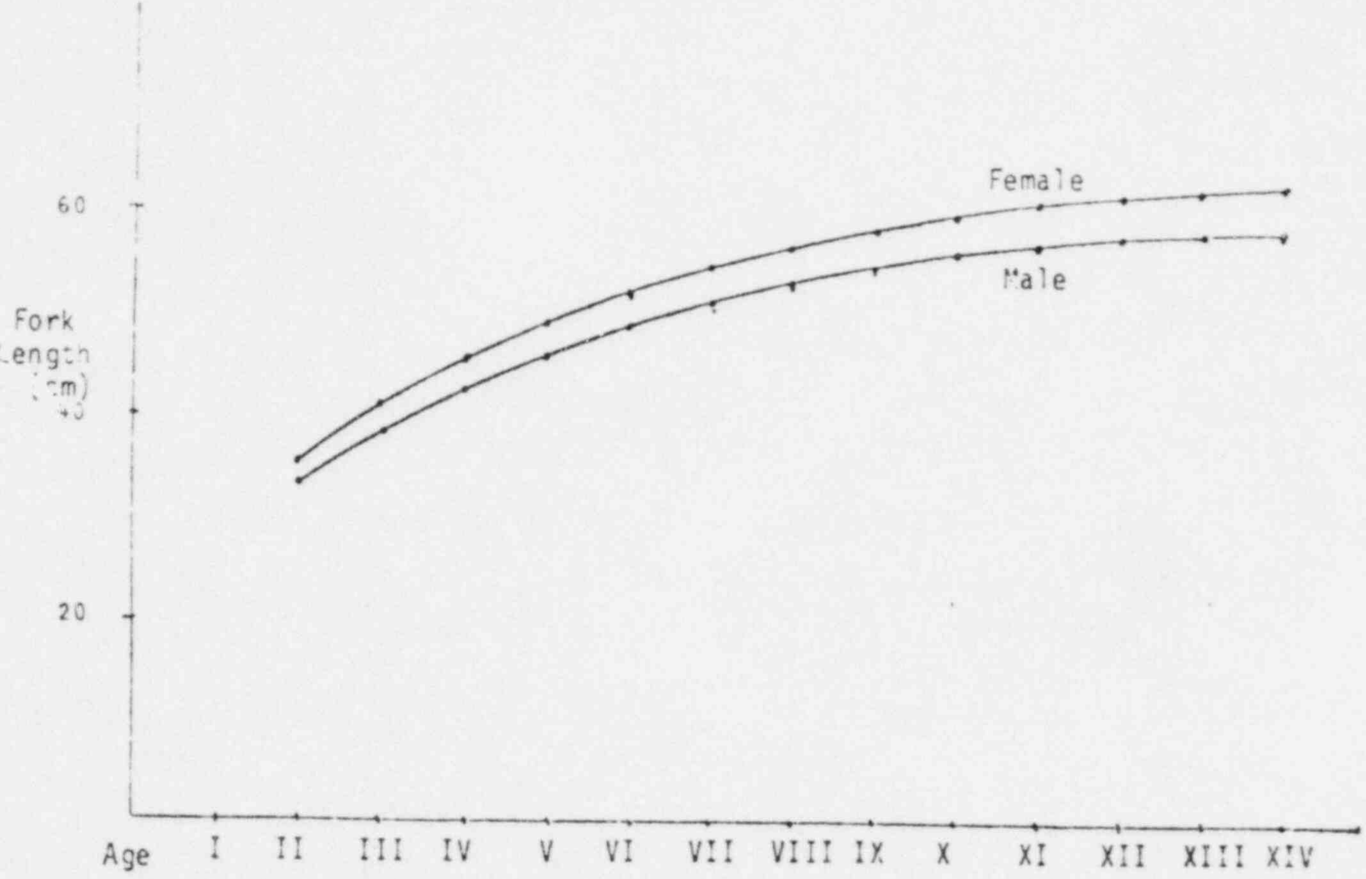

Figure 4. Estimates of average fork length (cm) by age group and sex according to the von Bertalanffy expression.

below with corresponding values of K and t_0:

	L_∞	K	t_0
males	57.06 cm	0.2655	-1.2847 yrs.
females	65.89 cm	0.1937	-1.9602 yrs.

The parameter (t_0) is used here as a scale adjustment to the empirical expression and is essentially devoid of any biological meaning.

Substituting the above parameters into equation 8 provides the following expression for males:

$$L_t = 57.06 \left[1-e^{-0.2655\,(t + 1.2847)}\right]$$

and for females:

$$L_t = 65.89 \left[1-e^{-0.1937\,(t + 1.9602)}\right]$$

for which are obtained the average fork length at age as shown in Columns 3 and 6 of Table 16. These computed fork lengths are compared with the observed values by sex in Columns 2 and 5 of Table 16. Computed lengths by sex are also graphically portrayed in Figure 4. These results demonstrate that the calculated length-age data conform closely with the observed values, and thus the employment of the von Bertalanffy growth model appears justified for the Connecticut River shad. Although these findings imply that females are always longer than males of the same age, the back-calculated length for age II males and for age II and III females may not be accurate, since during the immature stages there are likely to be major alterations in diet as well as marked seasonal variations in growth. For the present purpose, the requirements for a growth curve are: 1) the calculated growth in length and weight provides a satisfactory fit to observed growth data during the exploitable phase (age at first capture through the end of the life-span); and 2) it mathematically combines easily with other expressions.

To effectively analyze growth patterns of the shad population, it is essential to determine not only the length-age relationship, but the weight-age relationship as well. According to Beverton and Holt (1957), growth in weight (weight-age relationship) is denoted by the equation:

$$W_t = W\infty \left[1 - e^{-K\,(t-t_o)} \right]^n \qquad (13)$$

where W_t = weight in kilograms at age t (in years)

$W\infty$ = theoretical maximum weight corresponding to $L\infty$

n = exponent in the length-weight regression.

Before the above equation can be employed to determine the average weight at age, it is first necessary to compute the length-weight relationship separately for male and female shad. As mentioned earlier, average fork length and average weight by age group, sex, and fishery from 1974 - 1977 are shown in Tables 11 and 12.

These data were used to calculate a length-weight expression by sex according to the logarithmic linear regression:

$$\mathrm{Log}_{10} W_x = a + b\ \mathrm{Log}_{10} L_x \qquad (14)$$

where W_x = average weight (gr) at age x

L_x = average fork length (mm) at age x.

The length-weight relationship for male shad is shown as:

$$\mathrm{Log}_{10} W_x = -7.6030 + 2.9423\ \mathrm{Log}_{10} L_x$$

and for females:

$$\mathrm{Log}_{10} W_x = -7.8305 + 3.0200\ \mathrm{Log}_{10} L_x.$$

The slope (b) of the length-weight regressions for both sexes approaches a cube relation (3.0). This growth pattern is known as isometric growth and is characterized by a fish which gains weight in direct proportion to the cube of its length, and which maintains a stable specific gravity throughout its life (Ricker, 1975).

Table 17. Calculated[1/] and observed average weight (kg) by age and sex.

Males			Females		
(1) Age	(2) Obs. average weight	(3) Calc. average weight	(4) Age	(5) Obs. average weight	(6) Calc. average weight
II	-	0.572	II	-	0.764
III	0.941	0.902	III	-	1.175
IV	1.269	1.227	IV	1.632	1.606
V	1.534	1.522	V	2.035	2.032
VI	1.793	1.778	VI	2.404	2.435
VII	1.957	1.992	VII	2.926	2.805
VIII	-	2.167	VIII	3.064	3.137
IX	-	2.308	IX	-	3.429
X	-	2.420	X	-	3.683
XI	-	2.508	XI	-	3.901

1/ Calculated average weight at age was computed using von Bertalanffy growth model.

It should be noted that the slopes 2.9423 and 3.0200 for males and females respectively are equivalent to the exponent (n) of equation 13. Substituting the values for L∞ for males (57.06 cm) and females (65.89 cm) into the appropriate length-weight regression yields the corresponding maximum weights (W∞) which are 2.814 kg and 5.039 kg, respectively. Using equation 13, the expression of growth in weight (weight-age relationship) for males is:

$$W_t = 2.814 \left[1-e^{-0.2655\ (t\ +\ 1.2847)} \right]^{2.9423}$$

and for females is:

$$W_t = 5.039 \left[1-e^{-0.1937\ (t\ +\ 1.9602)} \right]^{3.0200.}$$

From these equations, the average age-specific weight is computed for males and females as shown in Column 3 and 6 of Table 17. These data are also compared to the observed average weight at age in Columns 2 and 5.

The results of growth analyses revealed a theoretical maximum fork length (cm) for males and females of 57.06 and 65.89 cm, respectively. In terms of length at age, shad of these sizes would correspond to a theoretical maximum age of about 14 years. Because shad greater than age X have not been reported from the Connecticut River at least during recent times, I contend that a contemporary life-span for Connecticut River shad of greater than about eleven years is probably unattainable. Thus, the estimates of L∞ presented herein may be biased upward due to the difficulty in aging scales from older and scarcer age groups. For example, errors in age determination of scales from ages VII and VIII may result in high length increments between L_t and L_{t+1}; this would make the annual growth rate (K) too low and the corresponding value of L∞ too high. Of course it is possible that the values of L∞ are realistic in an historical context because before the advent of commercial fishing, industrial pollution, and dams, shad could have survived to a much greater age. Moreover, large shad weighing from 12 to 14 lbs. (5.44 - 6.35 kg) have been occasionally reported from the Atlantic coast (Walburg and Nichols, 1967).

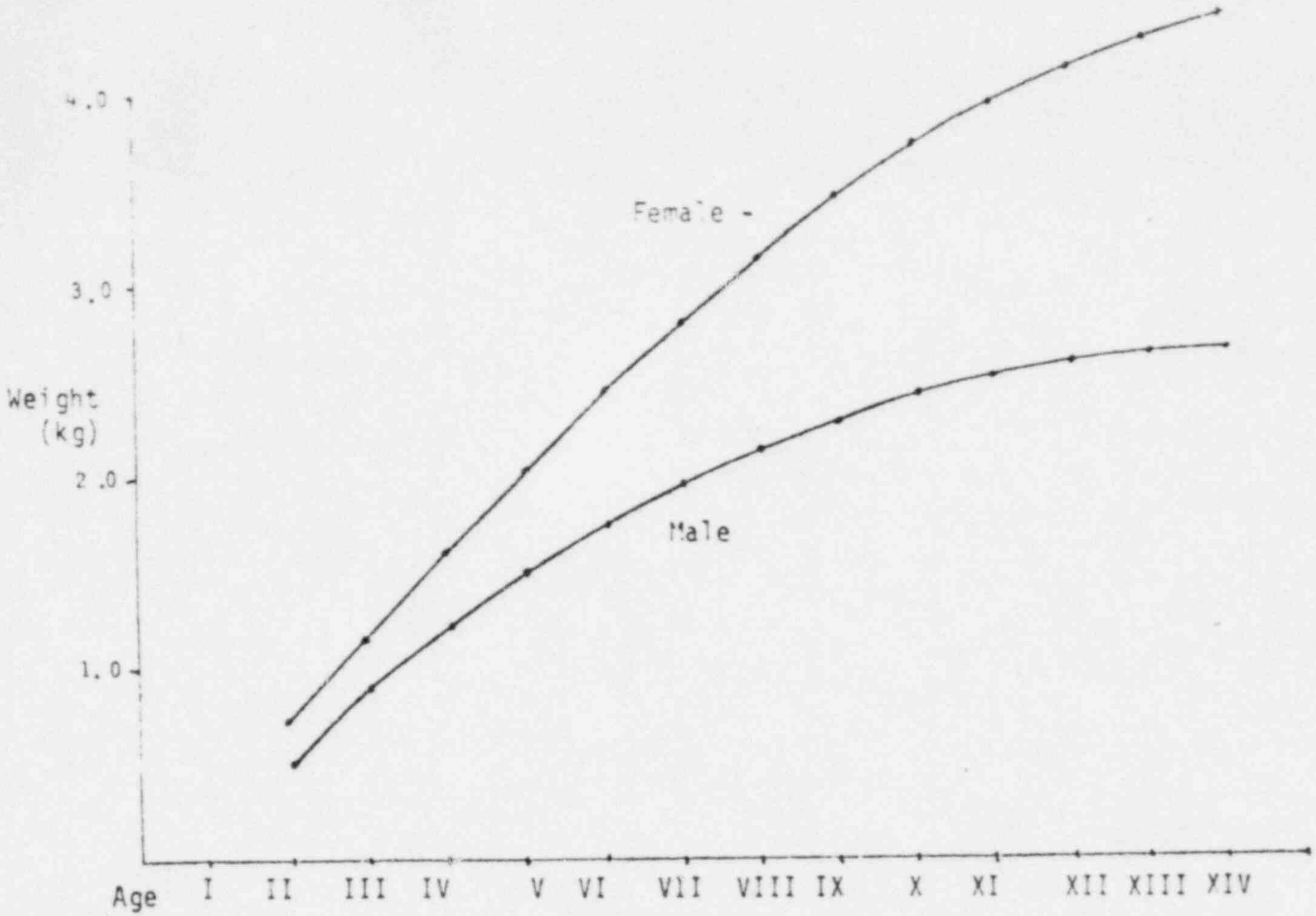

Figure 5. Estimates of average weight (kg) by age group and sex according to the von Bertalanffy expression.

There is some difficulty in using a model with a very high limit on growth especially if it is incorporated into a yield model without considering a realistic upper limit to the fishable life-span. An empirical life-span that is far beyond the limits of the observed estimates of length at age can lead to anomalous yield predictions. To realistically incorporate growth into the proposed yield model, the fishable life-span was terminated at age XI. This procedure possesses a certain element of realism because for many fish populations natural mortality increases considerably among mature and older fish (Ricker, 1949; Kennedy, 1954; Tester, 1955). Moreover, Greer-Walker (1970) indicated for the cod, Gadus morhua, that the myofibrils of the white muscles decrease in size with increasing age. Because the white muscles are responsible for acceleration in escape and attack, old fish may become more vulnerable to predators, fishing, disease, and less able themselves to find food. As for the shad, the physiological demands of spawning may become progressively greater with increasing age.

Figure 5 represents the estimated average weight (kg) at age for males and females, if the shad had always grown according to the von Bertalanffy expression. To utilize these parameters in a yield model, two conditions concerning the growth of shad are assumed true: 1) the parameters $W\infty$ and K will suffice to describe the the average weight gain from the age at first recruitment to the termination of life at age XI; and 2) the growth parameters $W\infty$ and K remain constant through time, and are not affected by density-dependent factors.

After determining these growth parameters, no consideration is given here to possible errors in determining growth from length-age or weight-age data. Such a bias could arise from selective mortality of the slower-growing individuals in a year-class owing to natural causes; or conversely, to selective retention of the faster-growing fish by the commercial and sport fisheries.

ESTIMATES OF FISHING AND NATURAL MORTALITIES

The yield from any fish population is largely dependent on the relationship between increments in weight due to growth and recruitment, and decrements in weight due to fishing and natural causes. Consequently, the correct mathematical formulation of total mortality and its component elements (fishing and natural mortalities) is essential to the basic comprehension of shad population dynamics, for accurate predictions of yield, and for rational management of both the commercial and sport fisheries. A fundamental tenet for computing total mortality is that the decline in numbers from a fish population approaches an exponential function such that a constant instantaneous mortality coefficient is operative. At this juncture it should be noted that all mathematical notations for mortality employed here are identical to those used by Ricker (1975). Because the forthcoming discussion requires the use of many mathematical expressions, I have listed in Table 18 the definitions of all mathematical notations used in this analysis.

Before the instantaneous rates of fishing (F) and natural (M) mortalities are estimated separately, it is convenient to compute first, the annual survival rate (S) and then the instantaneous rate of total mortality (Z). Using the stock estimates and the estimates of repeat spawners by sex, the annual survival rate (S) between consecutive years (t and t+1) is determined as follows:

$$S = \frac{R_{t+1}}{N_t} \qquad (15)$$

where R_{t+1} = numbers of repeat spawners by sex present in year t+1

N_t = numbers of virgin recruits and repeat spawners by sex present in year t.

The instantaneous total mortality (Z) is then calculated using the expression:

$$Z = -\ln S \qquad (16)$$

Table 18. Glossary of all mathematical notations used in the analysis of mortality.

Notation	Definition of Notation
Z	Instantaneous rate of total mortality
F_c	Instantaneous rate of fishing mortality due to commercial fishing
F_s	Instantaneous rate of fishing mortality due to sport fishing
F_{total}	Instantaneous rate of fishing mortality due to both commercial and sport fishing
M	Instantaneous rate of natural mortality
S	Annual rate of survival between successive years
u_c	Annual rate of fishing due to commercial fishing
u_s	Annual rate of fishing due to sport fishing
u_{total}	Annual rate of fishing due to both commercial and sport fishing
n	Annual rate of conditional natural mortality
v	Annual rate of natural mortality (between successive years)
N_t	Numbers of fish, by sex, present in year t
N_{t+1}	Numbers of fish, by sex, present in year t+1
P_{t+1}	Numbers of repeat spawners, by sex, present in year t+1
C_c	Numbers of fish, by sex, taken by commercial fishing in year t
C_s	Numbers of fish, by sex, taken by sport fishing in year t
D_t	Numbers of fish, by sex, lost to natural mortality between consecutive years
a_{t+1}	Proportion of repeat spawners by sex present in year t + 1

The concept of instantaneous rates and their relation to annual rates are discussed in detail by Ricker (1975, pages 8 - 18).

The estimates of mortality given in this report are average values for all year classes represented during two consecutive years. No attempt is made here to determine mortality rates for individual year classes throughout their fishable life. Such an analysis would require very accurate data on sex ratio, age composition, and stock size which I contend is beyond the capability of the present data.

In the present analysis, the following assumptions are implicit to the estimates of Z using equation 16: 1) the sex ratio of the annual run is approximately 50:50; 2) the population estimates are computed with a similar degree of accuracy each year; 3) the annual proportion of repeat spawners as determined from scale analysis is an unbiased estimate of the true proportion in the population; 4) all fish designated as repeat spawners had spawned during the previous year; and 5) all fish specified as virgin recruits had not spawned during the previous year. For the purposes of this investigation, assumptions 2, 4, and 5 are probably satisfied. As for assumption 3, I am forced to rely on the conditional supposition that the age structure and spawning history as derived from commercial and sport samples approach the true parameters in the population, since a more reliable method of estimating the true proportion is presently unavailable. Assumption 1 is the least tenable of the five; and the problems regarding the sex ratio of the shad population are discussed further below.

Though the hypothesis of a 50:50 sex ratio may be valid as a long-term approximation, it is doubtful whether the 1:1 ratio is maintained on an annual basis. Results from previous investigations are inconsistent regarding the sex ratio of adult shad, and further research is needed to better resolve

Table 19. Population estimates, commercial and sport catches by sex taken in year t; population estimates and numbers of repeat spawners by sex present in year t + 1; and numbers of male and female shad lost to natural mortality between year t and year t + 1, 1966 - 1977.

(1) Year	(2) Sex	(3) N_t Population	(4) C_c Comm. catch	(5) C_s Sport catch	(6) N_{t+1} Population	(7) R_{t+1} Repeat spawners	(8) D_t Shad dying of natural causes
1966	M	183,500	29,366	11,346	184,000	112,240	30,548
	F	183,500	51,467	11,346	184,000	84,640	36,047
1967	M	184,000	33,432	8,763	140,000	61,600	80,205
	F	184,000	42,532	8,763	140,000	32,200	100,505
1968	M	140,000	25,148	7,138	166,500	74,925	32,789
	F	140,000	33,025	7,138	166,500	49,950	49,887
1969	M	166,500	23,434	6,409	209,500	90,085	46,572
	F	166,500	45,333	6,409	209,500	69,135	45,623
1970	M	209,500	27,833	5,964	214,000	132,680	43,020
	F	209,500	43,534	5,967	214,000	57,780	102,219
1971	M	214,000	29,140	8,315	137,500	75,625	100,920
	F	214,000	45,578	8,315	137,500	37,125	122,982
1972	M	137,500	19,941	3,391	166,000	68,060	46,108
	F	137,500	31,256	3,391	166,000	76,360	26,493
1973	M	166,000	24,912	3,890	186,000	83,328	53,870
	F	166,000	43,622	3,890	186,000	59,148	59,340
1974	M	186,000	22,516	6,754	252,000	83,160	73,570
	F	186,000	38,993	6,754	252,000	50,148	90,105
1975	M	252,000	27,972	11,885	370,000	92,870	119,273
	F	252,000	47,628	11,885	370,000	58,460	134,027
1976	M	370,000	21,036	11,059	161,500	40,375	297,530
	F	370,000	85,725	11,059	161,500	23,902	248,314

Table 20. Annual proportion of repeat spawners by sex as determined from scale analysis, 1967 - 1977.

Year	Proportion of repeat spawners[1/]	
	Male	Female
1967	.610	.460
1968	.440	.230
1969	.450	.300
1970	.430	.330
1971	.620	.270
1972	.550	.270
1973	.410	.460
1974	.448	.318
1975	.33	.199
1976	.251	.158
1977	.250	.148

1/ Proportion of repeat spawners by sex from 1967 through 1973 was computed by Leggett (1976, Table 129, p. 208); those thereafter were calculated from Tables 9 and 10.

assumption 1. In the Connecticut River, studies conducted below the Holyoke Dam generally support the 50:50 sex ratio, whereas those performed above the dam and those from other rivers suggest a variable sex ratio. From 1967 - 1973, Leggett (1976) used drift gill nets at the mouth of the Connecticut River and revealed that the sex ratio during each year approximated 50:50. Likewise, Minta (personal communication) reported a sex ratio at the river mouth that approached 50:50 for the years 1974 - 1976; but in 1977, he indicated that the catch was composed of 82 percent females. For the sport fishery, 1958 - 1959, Nichols and Tagatz (1960) found a sex ratio that was close to 1:1. In contrast, Watson (1970) reported that the male-female ratio above Holyoke was 4.08:1 in 1969 and 2.4:1 in 1970. From 1971 - 1975, Scherer (1974) and Foote (1976) also indicated an unbalanced sex ratio favoring males. Yet for the years 1976 - 1977, Reed (personal communication) found a sex ratio above the dam that approached 50:50. In the Delaware River, Chittenden (1969) used haul seines and reported a sex ratio that varied considerably among years. He concluded that the observed deviations in the sex ratio were partly the result of differences in year class strength. In the Hudson River, Talbot (1954) used staked gill nets and reported a male-female ratio of 1:2 in 1950 and 1:1.5 in 1951. In addition, he employed drift gill nets further upriver and found a male:female ratio of 1.2:1 in 1950 and 1.7:1 in 1951.

From 1966 - 1976, population estimates (N_t) are separated according to the assumed 50:50 sex ratio and are shown in Column 3, Table 19. The adjusted commercial catches (C_c) separated by sex are given in Column 4. The sex ratios of these landings were determined from the summary reports prepared by the Connecticut Department of Environmental Protection (unpublished data). These reports contain not only the yields in numbers and weight by sex, but the average weights as well. As the catch data indicate, during most years the sex ratios are in favor of females by nearly 2:1. Though certain fishermen are suspected of selectively discarding males from their catches, no information concerning the discard rate is available.

From 1966 - 1973, the total sport catches (C_s) as determined by Leggett (1976) are shown in Column 5, Table 19. From Leggett's data, the catches from the entire sport fishery were, on the average, 2.327 times greater than the sport catches at Enfield. Thus, estimates of the total sport catches for the years 1974 - 1976 were obtained by multiplying the Enfield catches by 2.327. The sport catches from 1966 - 1976 were divided equally by sex, since a 50:50 sex ratio is in accord with the findings for the sport fishery by Nichols and Tagatz (1960) and Leggett (1976).

Numbers of repeat spawners (R_{t+1}) present from 1967 - 1977 are given in Column 7, Table 19. The R_{t+1} values were determined by sex using the following expression:

$$R_{t+1} = a_{t+1} N_{t+1} \qquad (17)$$

where a_{t+1} = proportion of repeat spawners by sex present in year t+1 (See Table 20)

N_{t+1} = estimated population size by sex present in year t+1 (Column 6, Table 19)

The numbers of adult shad (D_t) by sex lost to natural mortality between consecutive years is resolved by substituting for each sex the values N_t, C_c, C_s, and R_{t+1} into the following expression:

$$D_t = N_t - (C_c + C_s + R_{t+1}). \qquad (18)$$

The D_t values by sex are given in Column 8, Table 19. It should be noted that these values represent the loss in numbers due to all factors excluding the catches from the commercial and sport fisheries. Losses due to natural causes may occur as a result of the following factors: predation and disease at sea; commercial fishing outside the river; physiological exhaustion following spawning; Holyoke

Table 21. Annual rates of survival (S), fishing mortality (u) and natural mortality (v) by sex, 1966 - 1977.

(1)	(2)	(3)	(4)	(5)	(6)	(7)
Year	Sex	S Survival rate between t and t + 1	u_c Annual rate of comm. fishing	u_s Annual rate of sport fishing	u_{total} Annual rate of all fishing	v Annual rate of natural mortality between t an t + 1
1966	M	0.6117	0.1600	0.0736	0.2218	0.1665
	F	0.4613	0.2805	0.0859	0.3423	0.1964
1967	M	0.3348	0.1817	0.0582	0.2293	0.4359
	F	0.1750	0.2312	0.0619	0.2788	0.5462
1968	M	0.5352	0.1796	0.0621	0.2306	0.2342
	F	0.3568	0.2359	0.0667	0.2869	0.3563
1969	M	0.5411	0.1407	0.0448	0.1792	0.2797
	F	0.4152	0.2723	0.0529	0.3108	0.2740
1970	M	0.6333	0.1329	0.0328	0.1613	0.2053
	F	0.2758	0.2078	0.0360	0.2363	0.4879
1971	M	0.3534	0.1362	0.0450	0.1750	0.4716
	F	0.1735	0.2130	0.0494	0.2518	0.5747
1972	M	0.4950	0.1450	0.0288	0.1697	0.3353
	F	0.5553	0.2273	0.0319	0.2520	0.1927
1973	M	0.5020	0.1501	0.0276	0.1735	0.3245
	F	0.3563	0.2628	0.0318	0.2862	0.3575
1974	M	0.4471	0.1211	0.0413	0.1574	0.3955
	F	0.2696	0.2096	0.0459	0.2460	0.4844
1975	M	0.3685	0.1110	0.0531	0.1582	0.4733
	F	0.2320	0.1890	0.0582	0.2362	0.5319
1976	M	0.1091	0.0569	0.0317	0.0867	0.8041
	F	0.0646	0.2344	0.0390	0.2643	0.6711

Table 22. Instantaneous rates of total mortality (Z), fishing mortality (F) and natural mortality (M) by sex, 1966 - 1977.

(1)	(2)	(3)	(4)	(5)	(6)	(7)
Year	Sex	Z Total mortality	F_c Comm. fish mortality	F_s Sport fish mortality	F_{total} Total fish mortality	M Natural mortality
1966	M	0.4915	0.1744	0.0765	0.2509	0.2406
	F	0.7737	0.3292	0.0899	0.4190	0.3547
1967	M	1.0942	0.2005	0.0600	0.2605	0.8337
	F	1.7430	0.2629	0.0639	0.3268	1.4162
1968	M	0.6251	0.1980	0.0642	0.2622	0.3629
	F	1.0306	0.2690	0.0691	0.3381	0.6925
1969	M	0.6142	0.1517	0.0458	0.1975	0.4167
	F	0.8790	0.3178	0.0543	0.3722	0.5068
1970	M	0.4568	0.1425	0.0334	0.1759	0.2809
	F	1.2881	0.2329	0.0366	0.2696	1.0185
1971	M	1.0402	0.1464	0.0460	0.1924	0.8478
	F	1.7516	0.2395	0.0506	0.2901	1.4615
1972	M	0.7032	0.1567	0.0293	0.1860	0.5172
	F	0.5883	0.2579	0.0324	0.2903	0.2980
1973	M	0.6892	0.1626	0.0280	0.1906	0.4986
	F	1.0320	0.3049	0.0323	0.3372	0.6948
1974	M	0.8050	0.1290	0.0422	0.1712	0.6338
	F	1.3108	0.2353	0.0470	0.2823	1.0285
1975	M	0.9983	0.1177	0.0545	0.1722	0.8261
	F	1.4610	0.2095	0.0599	0.2694	1.1916
1976	M	2.2155	0.0585	0.0322	0.0907	2.1248
	F	2.7395	0.2671	0.0398	0.3069	2.4326

sport fishery; and inability to descend from above the Holyoke Dam.

An example of the computation for survival (S) and total mortality (Z) for male shad between 1966 and 1967 is given below. The total 1967 population was estimated as 368,000 individuals (Column 3, Table 19); assuming a 50:50 sex ratio, an estimate of 184,000 fish of each sex is obtained. During 1967, 61 percent of the males sampled were repeat spawners (Table 20). Consequently, the proportion of repeat spawning males (R_{t+1}) present in the 1967 population is computed using equation 17 as follows:

$$112{,}240 = 0.61\ (184{,}000).$$

Given the total population of males (183,500) in 1966 and the numbers of repeat spawning males (112,240) present in 1967, male survival rate (S) between 1966 and 1967 is then calculated using equation 15 as follows:

$$S = \frac{112240}{183500} = 0.6117.$$

The corresponding instantaneous rate of total mortality (Z) is obtained by utilizing expression 16 as follows:

$$Z = -\ln 0.6117 = 0.4915$$

From 1966 - 1977, annual survival rates (S) by sex are shown in Column 3, Table 21, while instantaneous rates of total mortality Z are divided by sex in Column 3, Table 22.

From the annual population estimate (N_t) and the annual commercial landing (C_c) by sex (Columns 3 and 4, Table 19), the annual fishing rate due to commercial fishing (u_c) can be obtained at once from the following expression:

$$u_c = C_c/N_t. \qquad (19)$$

Because the commercial fishery is situated some 60 km downriver from the sport fishing areas, the shad entering the river are subjected first to the gill net fishery and then later to the sport fishery. Accordingly, the annual fishing rate (u_s) due to the sport fishery is computed by substituting the estimate (C_s)

of the sport catch (Column 5, Table 19) into the following equation:

$$u_s = C_s / (N_t - C_c). \qquad (20)$$

The annual rate of fishing (u_{total}) resulting from both fisheries combined is obtained by the expression:

$$u_{total} = u_c + u_s - (u_c u_s), \qquad (21)$$

which is equivalent to:

$$(C_c + C_s)/N_t.$$

The product ($u_c u_s$) is an essential component in equation 21 because the probability of catching a shad at the sport fishing areas depends upon the intensity of the commercial fishery located 60 km downriver. In other words, the sport fishery exploits only that portion of the run not taken by the commercial fishery. The annual rates of fishing due to each fishery (u_c and u_s) and for both fisheries combined (u_{total}) are given by sex in Columns 4, 5 and 6 of Table 21.

Once the annual fishing rate (u) is obtained, the corresponding instantaneous rate (F) can be determined for the respective fisheries. Yet, according to Ricker (1975), the proper mathematical expression for calculating F depends upon whether fishing occurs seasonally or throughout the year. Because the commercial and sport fisheries generally commence in April and extend through May, they are both categorized as seasonal fisheries. Thus, it is appropriate to begin the biological year in April and to consider that natural mortality occurs after fishing ends. This is a realistic assumption for two reasons: 1) an adult shad cannot be lost to both fishing and natural causes, and 2) the fishing effort is sufficiently intense during April and May, so that natural mortality during that period should be minimal. This concept of a seasonal fishery is of particular importance, since differences in the seasonal incidence of fishing and natural mortality can greatly influence the relative dimensions of F and M.

The F values by sex due to sport (F_s) and commercial (F_c) fishing are determined by substituting the corresponding annual rate of fishing (u_s and u_c) into the following expression:

$$F = -\ln(1-u) \qquad (22)$$

According to Ricker (1975), instantaneous rates of mortality are always additive such that:

$$F_{total} = F_c + F_s. \qquad (23)$$

Values of F_c, F_s, and F_{total} are shown in Columns 4, 5 and 6 of Table 22.

Given the instantaneous rates of fishing (F_{total}) and total mortality (Z), the instantaneous rates of natural mortality (M) are estimated by sex using simple subtraction:

$$M = Z - F_{total}. \qquad (24)$$

Values of M according to sex are presented in Column 7 of Table 22.

To obtain the corresponding rates of annual natural mortality (v), it is first necessary to determine the conditional rate of natural mortality (n) using the following expression:

$$n = 1 - e^{-M} \qquad (25)$$

The conditional rate (n) is defined as the proportion of the annual run which would be lost due to natural causes if fishing did not occur. Once n is known, the values of (v) by sex is computed as follows:

$$v = n\,(1 - u_{total}), \qquad (26)$$

which is identical to:

$$D_t/N_t.$$

Annual rates of natural mortality (v) are assembled by sex in Column 7 of Table 21.

Instantaneous rates of total mortality (Z) by sex occurring between consecutive years from 1966 through 1977 are depicted in Figures 6 and 7. During most years,

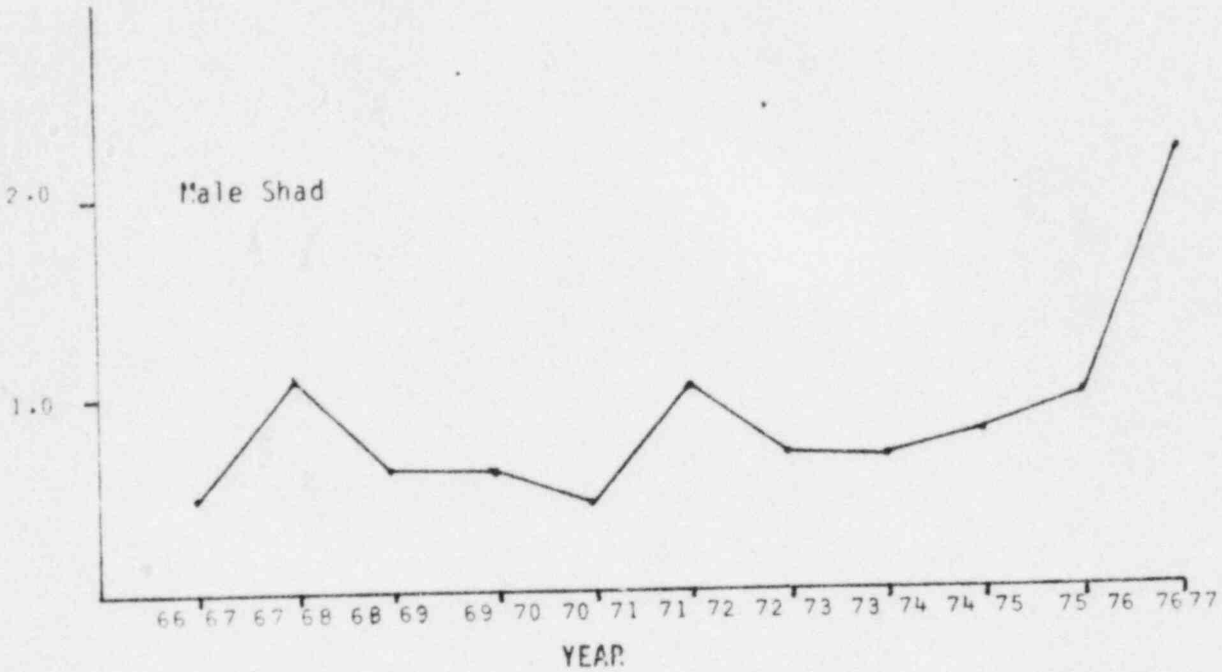

Figure 6. Estimates of the instantaneous total mortality rate (Z) for male shad during the period 1966-1977.

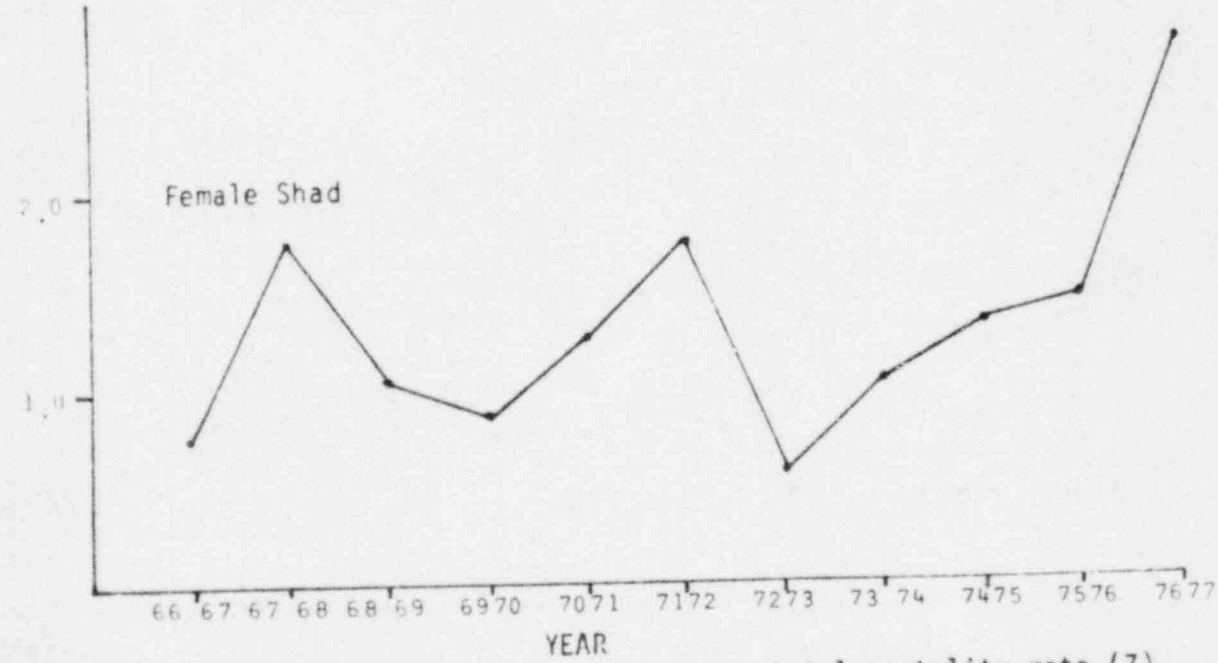

Figure 7. Estimates of the instantaneous total mortality rate (Z) for female shad during the period 1967-1977.

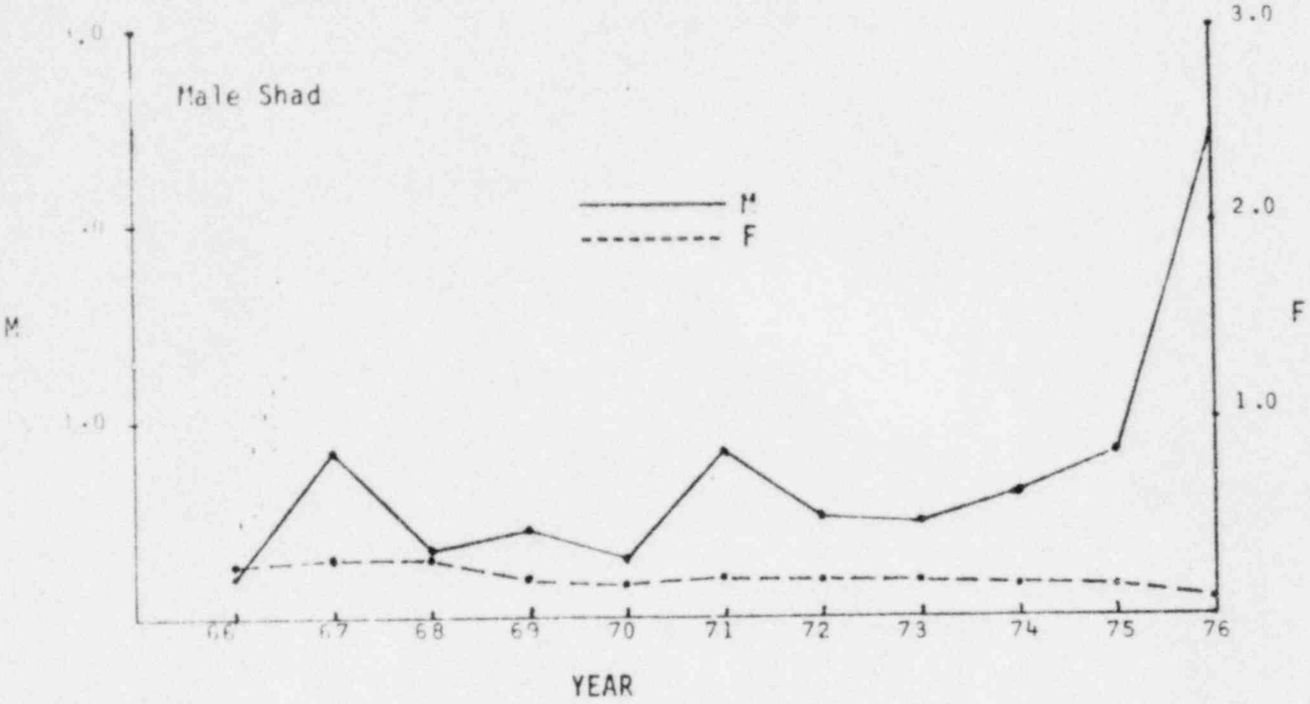

Figure 8. Relationship between the instantaneous natural (M) and fishing (F) mortality rates for male shad during the period 1966-1976

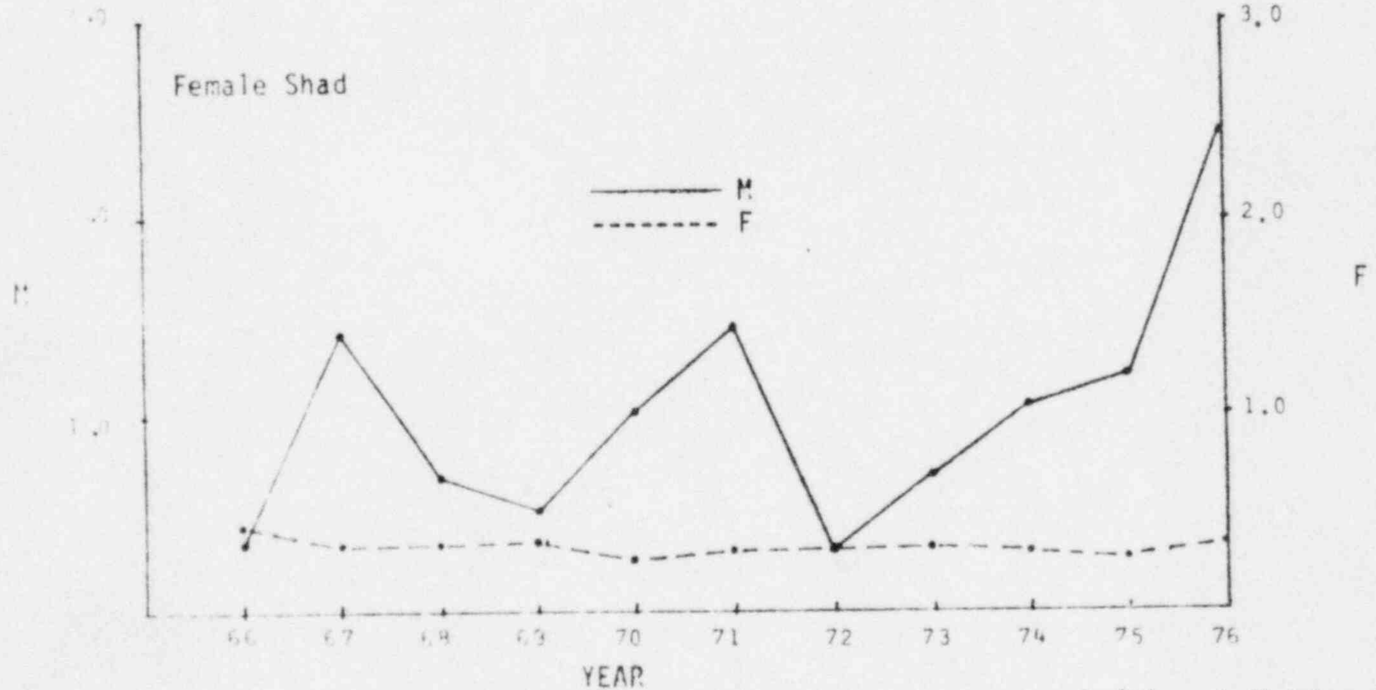

Figure 9. Relationship between the instantaneous natural (M) and fishing (F) mortality rates for female shad during the period 1966-1976

Table 23. Mean ($\bar{x}$)[1/] and standard deviation (s_x) for the instantaneous rates of total (Z) and natural (M) mortalities and annual rates of survival (S) and mortality (v) by sex for the period 1966 - 1974.

		(1)	(2)	(3)	(4)
		(Z) Instantaneous total mortality	(S) Annual survival	(M) Instantaneous natural mortality	(v) Annual rate of natural mortality
	Males				
Mean	($\bar{x}$)	0.7244	0.4846	0.5147	0.3264
S. D.	(s_x)	0.2215	0.1028	0.2207	0.1049
	Females				
Mean	($\bar{x}$)	1.1552	0.3150	0.8302	0.4079
S. D.	(s_x)	0.4058	0.1281	0.4284	0.1453

[1/] Average estimates of (Z) and (M) from 1966 - 1974 are taken from Column 3 and 7, Table 22, whereas average estimates of (S) and (v) from 1966 - 1974 are taken from Column 3 and 7, Table 21.

Table 24. Mean $(\bar{x})$[1/] and standard deviation $(s_{\bar{x}})$ for the instantaneous (F) and annual (u) rates of fishing by sex during the period 1966 - 1974.

	(1)	(2)	(3)	(4)	(5)	(6)
	(F_c) Instantaneous fishing mortality commercial	(F_s) Instantaneous fishing mortality sport	(F_{total}) Instantaneous fishing mortality sport and commercial combined	(u_c) Annual fishing rate commercial	(u_s) Annual fishing rate sport	(u_{total}) Annual fishing rate sport and commercial combined
Males						
$\bar{x}$	0.1624	0.0473	0.2097	0.1497	0.0460	0.1887
$s_{\bar{x}}$	0.0244	0.0167	0.0371	0.0206	0.0158	0.0298
Females						
$\bar{x}$	0.2722	0.0528	0.3250	0.2378	0.0514	0.2768
$s_{\bar{x}}$	0.0370	0.0191	0.0485	0.0276	0.0179	0.0344

[1/] Average estimates of (F) from 1966 - 1974 are taken from columns 4 - 6, Table 22, whereas average estimates of (u) from 1966 - 1974 are taken from columns 4 - 6, Table 21.

both the amplitude and variability of Z are greater for females than for males. The highest Z values for both sexes occurred during 1976/77, whereas the lowest values were found during 1970/71 for males and during 1972/73 for females.

Both the instantaneous rates of fishing (F_{total}) and natural mortality (M) by sex are graphically portrayed in Figures 8 and 9, respectively. The F_{total} levels exhibit little annual variation but are always greater for females, whereas the M values are highly variable and likewise are greater for females. The levels of M for both sexes generally follow the same trend with time as the Z values in Figures 6 and 7.

Because the passage of large numbers of adult shad over the Holyoke Dam from 1975 and thereafter may influence the rate of natural mortality (M), the best historical estimate of the parameters Z, M, S, and v by sex is the average value for the years 1966 - 1974 when less than 70,000 adult shad were transported over the dam. Average estimates of these parameters by sex are shown in Table 23. Results revealed that both the average total (Z) and natural (M) mortalities were greater for females ($Z = 1.1552$, $M = 0.8302$) than for males ($Z = 0.7244$, $M = 0.5147$). Thus, male shad have a greater between year survival rate ($S = 48.46$ percent) than do females ($S = 31.50$ percent) which is consistent with the occurrence of greater numbers of repeat spawning males between consecutive years (Column 7, Table 19).

From 1966 - 1974, the average instantaneous (F) and annual (u) fishing mortalities by sex and fishery are shown in Table 24. The average instantaneous rate of fishing (F_c) due to commercial fishing was greater for female shad (0.2722) than for males (0.1624), suggesting that gill nets select by sex. But for the sport fishery, the average F_s value is also greater for females (0.0528) than for males (0.0473), indicating that anglers select for female shad as well. The higher average F_s value for females superficially appears to conflict with the previous supposition of a 50:50 sex ratio for the sport catches. However, because the commercial gear apparently selects for female shad, the sex ratio of the remaining population that reaches the sport fishing areas is altered in favor of males. Consequently, the presence of a 50:50 sex ratio for sport catches actually shows that anglers preferentially retain female shad, and thus is perfectly compatible with the average F_s values (Column 2 Table 24). This conclusion is substantiated by Leggetts observation that during the peak of the run many anglers will retain females over males because of their roe, and because of their "trophy" size.

The average rates of instantaneous total mortality (Z) by sex (Column 1, Table 23) are similar to those reported by Leggett (1976, Table 134, p. 210) only after his 1965 data are excluded. From 1966 - 1973, he computed average Z as 1.001 for males and 1.159 for females as compared to 0.7244 and 1.1552 in this study. There are three principal reasons for the differences in Z, particularly among males. First, Leggett estimated Z for individual year classes, whereas I determined Z as an average value for all year classes present between two consecutive years.

Secondly, Leggett assumed that the sex ratios of the commercial catches were similar to those from his experimental catches taken at the river mouth (1967 - 1973). These experimental catches suggested a sex ratio that approached 50:50 (Leggett, 1976, Table 127, p. 205). However, his hypothesis regarding sex ratios for commercial catches may be invalid because Leggett tagged shad using drift gill nets with a mesh size of 13.7 cm (stretch measure), whereas the commercial fishermen used gill nets with mesh size ranging from 14.0 to 14.9 cm (stretch measure). Because female shad are longer and heavier than males at a given age, the nets employed by the fishermen will select for greater numbers of females than will the nets used by Leggett. As a result, the sex ratios (1967 - 1973) from the experimental nets may not be comparable to those taken from the commercial fishery. Consequently, his average estimates of annual fishing mortality (u_{total}) for male (22.4 percent) and female (23.5 percent) are incorrect.

Thirdly, Leggett reported average instantaneous rates of fishing (F_{total}) as 0.38 for males and 0.41 for females for the period 1965 - 1973. Given that the instantaneous rate of fishing (F) is expressed by the equation:

$$F = pn$$

where p = the catchability coefficient (constant)

n = total fishing effort (SFU),

the levels of F as derived by Leggett (1976, Table 136, p. 211) are too high and are inconsistent with his catchability coefficient (0.000180) and his estimates of effort (SFU) from 1965 - 1973.

From 1956 - 1959, Walburg (1961) computed the age structure and spawning history of adult shad and reported an average Z of 1.31 for both sexes combined. He also determined an average annual fishing (u_c) rate of 36 percent and an average rate of annual natural mortality (v) of 58 percent. Yet the 58 percent is actually the conditional rate of natural mortality (n) since he failed to consider the seasonal nature of the commercial fishery. The annual natural mortality rate (v) is determined by using equation 26 as follows:

$$v = 0.58\ (1 - 0.36) = 0.37.$$

Thus, his rate of natural mortality (37 percent) is very similar to the average v for males (32.64 percent)and females (40.79 percent) in Column 4, Table 23.

Using the levels of escapement during 1946 and 1947, Fredin (1954) estimated annual natural mortality (v) for age VI shad between years. Unlike Leggett (1976) and Walburg (1961), Fredin considered the seasonal nature of the commercial and sport fisheries before he computed the level of natural mortality. His results revealed an annual rate of natural mortality (v) of 36.3 percent for both sexes combined which is in close agreement with my average estimate of 36.7 percent (Column 4, Table 23).

EFFECTS OF GEAR SELECTIVITY ON THE ESTIMATES OF MORTALITY (Z) AND SURVIVAL (S)

Although the estimates of mortality furnished in the previous section are calculated using valid mathematical techniques, certain inconsistencies do exist with these estimates which can only be resolved with further research. As an example, the conclusion that average annual survival of males is higher than that for females is in conflict with the assumed 50:50 sex ratio of the population. In the first place, higher between year survival for males would inevitably alter the sex ratio in favor of males. Under these conditions, the 1:1 sex ratio could be maintained only if survival to the recruited phase constantly favored female shad. During certain years, virgin females would be expected to outnumber males due to deviations in the strength of incoming year classes. Yet it is doubtful that recruitment favoring females could be continually maintained especially since immature females of a year class are exposed to an additional year of oceanic mortality before becoming sexually mature.

The reasons for the anomally regarding higher male survival and the assumed 50:50 ratio are unknown. My contention is that natural mortality estimates (M) for males are too low due to a combination of the following factors: 1) the sex ratio of the annual shad run is not always 50:50, but varies according to the relative strength and weakness of recruited year classes; and 2) the age structure and spawning history for males as derived from commercial and sport samples are biased in favor of longer and older individuals.

As for the first factor, I mentioned previously (see page 77) that the assumed 50:50 sex ratio should be regarded as an approximate value until further research could provide a more exact value. However, if the sex ratios among years deviate in a random rather than a systematic manner, then the degree of bias would cancel out, and the average mortality estimates for males would not be seriously affected by variations in the sex ratio.

Table 25. Estimates of annual fishing mortality (u_c) for adult shad tagged and recaptured by sex and by size groups, April - May, 1976.

Males

Size groups (fork length, cm)

	34-44	45	46	47	48	49	50-53	Total
Not recaptured	466	356	401	282	183	118	83	1889
Recaptured	28	41	54	39	22	15	16	215
Total	494	397	455	321	205	133	99	2104
u_c	0.06	0.10	0.12	0.12	0.11	0.11	0.16	0.10

Females

Size groups (fork length, cm)

	32-44	45	46	47	48	49	50	51	52	53-57	Total
Not recaptured	43	97	194	365	477	354	274	143	80	80	2107
Recaptured	3	11	21	65	82	82	60	24	15	20	383
Total	46	108	215	430	559	436	334	167	95	100	2490
u_c	0.07	0.10	0.10	0.15	0.15	0.19	0.18	0.14	0.16	0.20	0.15

Table 26. Estimates of annual fishing mortality (u_c) for adult shad tagged and recaptured by sex and by size groups, April - May, 1977.

Males

Size groups (fork length, cm)

	32-44	45	46	47	48	49	50-54	Total
Tagged not recaptured	199	110	133	105	79	56	60	742
Recaptured	9	11	14	17	18	13	12	94
Total tagged	208	121	147	122	97	69	72	836
u_c	0.04	0.09	0.10	0.14	0.19	0.19	0.17	0.11

Females

Size groups (fork length, cm)

	32-44	45	46	47	48	49	50	51	52	53	54	55-60	Total
Tagged not recaptured	52	92	200	318	414	476	624	416	260	104	43	38	3047
Recaptured	5	20	40	84	113	136	206	156	92	46	10	4	912
Total tagged	67	112	240	402	527	612	830	572	352	150	53	42	3959
u_c	0.07	0.18	0.17	0.21	0.21	0.22	0.25	0.27	0.26	0.31	0.19	0.10	0.23

The second source of bias is more important than the first because the accuracy of the total mortality (Z) and survival (S) estimates are largely dependent upon the reliability of the age composition and spawning history. If the gill net fishery should select for the larger males of the population, then the age composition data would contain too few smaller and younger virgin males.

To determine whether the gill net fishery selects for females and for larger males, the numbers of shad tagged and later recaptured during the spring of 1976 and 1977, were partitioned by sex and fork length and assembled in Tables 25 and 26. During 1976, of the 2,104 males tagged at the river mouth, 215 were recaptured and reported by the commercial fishery (Table 25). The annual fishing rate (u_c) for males was then computed using the following expression:

$$u_c = \frac{R_t}{M_t}$$

where R_t = total numbers of fish by sex recaptured in year t

M_t = total numbers of fish by sex tagged at the river mouth in year t.

Accordingly, u_c for males was determined as 10 percent by substituting the values 2104 (M_t) and 215 (R_t) into the above equation. For females 2490 individuals were tagged at the river mouth, 383 of which were subsequently recaptured (Table 25). The fishing rate (u_c) for females was computed as 15 percent. The fishing rates of 10 and 15 percent were transformed into a 40:60 proportion, and then analyzed by Chi square to determine whether the observed proportion differed significantly from 50:50. The results revealed a significant departure from a 50:50 proportion favoring females (X^2 = 4.00, d.f. = 1, $P<0,05$). This serves as presumptive evidence that the gill net fishery selects for females over males.

In 1977, 836 males and 3,959 females were tagged at the river mouth (Table 26) and commercial fishermen later submitted 94 male tags and 912 female tags. The fishing rates (u_c) were then computed as 11 percent for males and 23 percent for females. These u_c values were transformed into a 32:68 proportion and then analyzed by Chi square. Results for the 1977 data showed a significant departure from a 50:50 proportion favoring females(X^2 = 12.96, d.f. = 1, $p<0.001$). This further vindicates the findings from the previous analysis. The fishing rates (u_c) as determined from tag-recapture data, 1976-1977, are of particular interest since they exemplify the conscious effort by the commercial fishermen to selectively retain females over males by almost a 2:1 ratio. Moreover, these findings are compatible with most of the sex ratios of commercial catches given in column 4 of Table 19. By pooling the u_c values by sex for the years 1976-1977 and by utilizing equation 22 (see page), F_c values for male and female shad were calculated as 0.1109 and 0.2107, respectively. These values are similar to those shown in Column 4 of Table 22.

Fishing rates (u_c) by sex and fork length are given in Row 4 of Tables 25 and 26. In 1976, 494 small males (fork length 34 - 44 cm) were tagged and 28 were later recaptured (Table 25); representing a u_c of 6 percent. In contrast, u_c for males greater than 46 cm ranged from 11 - 16 percent with complete retention occurring at lengths between 50 and 53 cm. In 1977, 208 small males (fork length 32 - 44 cm) were tagged, 9 of which were recaptured (Table 25), representing a u_c of 4 percent. For males greater than 46 cm, u_c ranged from 14 to 19 percent. However, unlike the 1976 data, complete retention among male shad apparently did not occur in 1977 since male u_c values at a given length are always smaller than those for females. These data from 1976 - 1977 suggest that males of age group III, IV and V (approximate for lengths, 35 - 46 cm) are completely retained in the drift gill nets. Accordingly, male scale samples collected from the commercial fishery will contain a paucity of smaller and younger virgins, and an inordinately high number of longer and older repeat spawners.

The u_c estimates for females in 1976 increase steadily with fork length up to 49 cm; they decline slightly at 50 and 51 cm, then increase again from 52 to 57 cm (Table 25). Likewise in 1977, u_c for females increase with increasing fork length up to 53 cm, and then they decline slightly thereafter (Table 26). However, unlike the males, females as small as 47 cm approach full retention. The female data certainly suggest that girth is more important than length for determining the extent of selection in the gill net fishery.

For the sport fishery, the higher F_s values for females (Column 2, Table 24) and the presence of an approximate 50:50 sex ratio for the catches (Leggett, 1976) demonstrates that anglers also select for females. Moreover, it is entirely possible that during the peak of the run sport fishermen not only select for females, but for larger males as well. As a result, the age composition and spawning history for males would also contain too many repeat spawners. When the data from both fisheries are combined, the proportion of repeat spawners is biased upward resulting in estimates of survival (S) which are too high, and corresponding estimates of total mortality (Z) which are too low. As stated previously, total mortality (Z) is equivalent to fishing (F_{total}) plus natural mortality (M). The estimates of fishing mortality (F_{total}) for males are unbiased because they were computed in a manner which is independent of the age composition data. Thus it is the natural mortality estimates (M) which are underestimated. My suspicions regarding the inordinately low rates of natural mortality (M) among male shad are substantiated by Whitney's (1961) findings that mortality of Susquehanna River shad between 1958 - 1959 and between 1959 - 1960 was consistently higher for males than for females.

In contrast, age composition and spawning history data for females are far more representative of the true parameters of the population because most female shad (i.e. greater than 46 cm) are fully retained in the gear employed by commercial fishermen (Tables 25 and 26). Consequently, estimates of female survival (S) and natural mortality (M) should be considerably more reliable than those for males.

To further test whether non-random sampling for age determination had biased the male estimates of mortality and survival, a sampling method would have to be established that was neither selective by sex nor length. A pound net set annually at the river mouth may provide more reliable data regarding the age structure, spawning history, and sex ratio of the shad population. Moreover, the age structure as derived from pound net samples could be compared to those from commercial and sport samples to confirm or refute the hypothesis that both fisheries select for females and for larger male shad.

RELATIONSHIP BETWEEN THE NUMBERS OF SHAD TRANSPORTED OVER THE HOLYOKE DAM FROM 1966 - 1977 AND ESTIMATES OF NATURAL MORTALITY (M)

The numbers of male and female shad annually lifted over the Holyoke Dam from 1966 - 1977 are illustrated with the corresponding levels of M in Figures 10 and 11. The graphs for both sexes demonstrate that the highest rate of natural mortality (M) occurred during 1976/77 coincident with the passage of almost 350,000 adult shad over Holyoke. To determine whether a statistically significant relationship existed between the levels of M and the numbers of adults lifted at Holyoke, linear regression analysis was conducted for each sex. Results revealed that the correlation coefficient for males ($r = 0.872$, $t = 5.34$, d.f. = 9, P 0.001) and females ($r = 0.803$, $t = 4.04$, d.f. = 9, $P<0.01$) was significant. The linear regression equation for males is:

$$M = 0.2626 + 0.00000912X_t,$$

and for females is:

$$M = 0.7439 + 0.0000105X_t$$

where M = estimated rate of instantaneous natural mortality (M)

X_t = numbers of adults by sex lifted at Holyoke during year t.

It should be noted that both an exponential function and a power function of the types

$$M = ae^{bX_t}$$

and

$$M = aX_t^{\,b}$$

were also fitted to the above data, but both functions produced correlation coefficients that were lower than those from linear regression analysis. Therefore, this analysis provide presumptive evidence that natural mortality increases in a linear function when increasing numbers of adult shad are passed over Holyoke. This conclusion would explain the noticeable decline in the size of the shad run from 740,000 individuals in 1976 to 64,000 repeat spawners in 1977. Moreover,

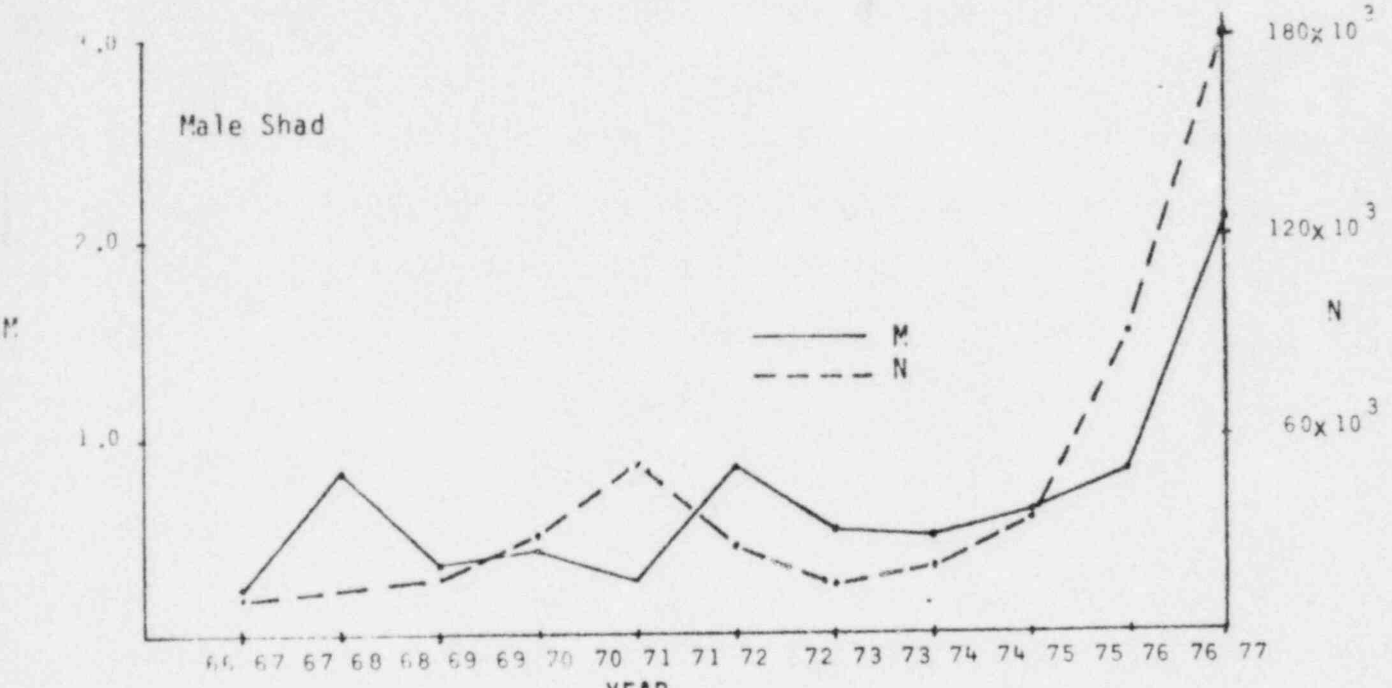

Figure 10. Relationship between changes in the male instantaneous rate of natural mortality (M) and variations in the numbers of male shad lifted at Holyoke, 1966-1977

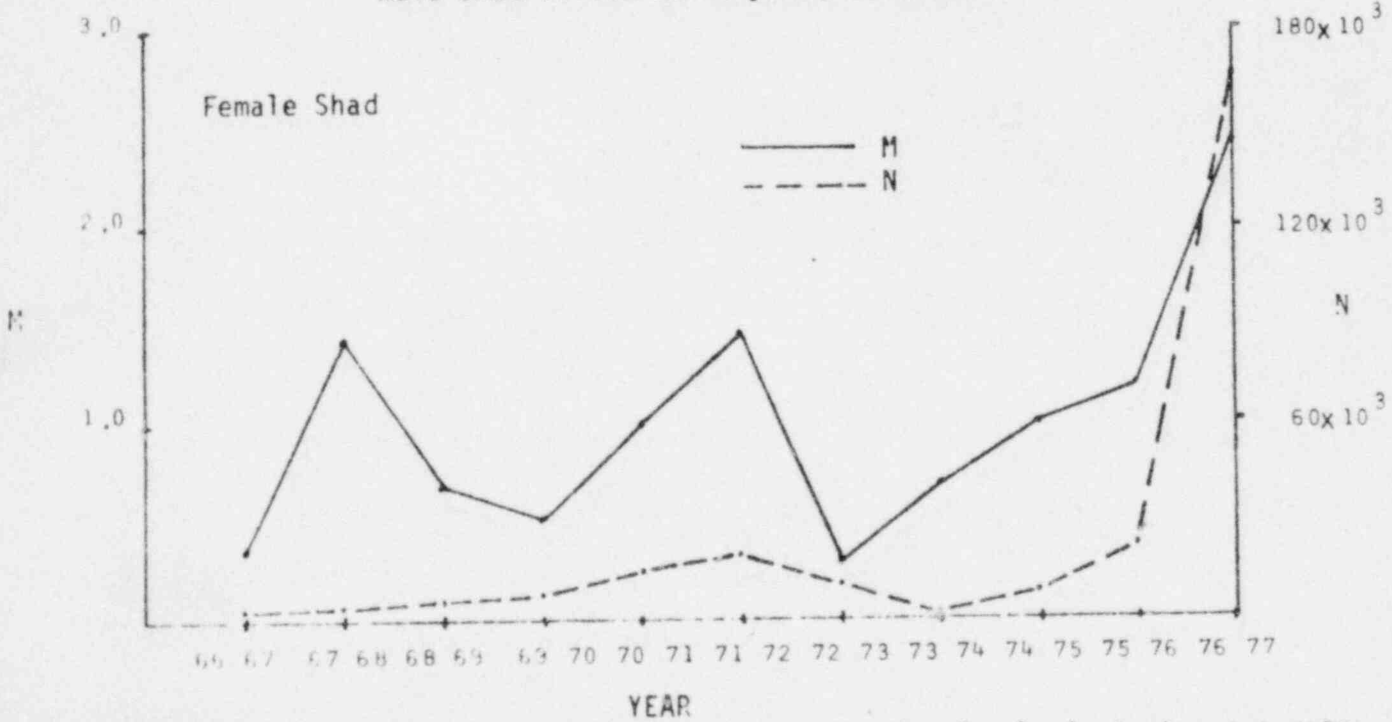

Figure 11. Relationship between changes in the female instantaneous rate of natural mortality (M) and variations in the numbers of female shad lifted at Holyoke, 1966-1977

these results are supported by the tagging study conducted by Whitney (1961) in the Susquehanna River. During the spring of 1958 and 1959, adult shad were tagged from above and below the Conowingo Dam to determine whether natural mortality was greater for fish planted above this facility. In 1959 and 1960, fishermen recaptured some 3.5 percent of the fish tagged from below the dam, but only 0.3 percent of those tagged from above. As a result Whitney concluded that the rate of natural mortality was higher for adult shad lifted over the Conowingo Dam.

Although this analysis establishes a positive association between natural mortality and the passage of fish over Holyoke, the exact mechanism by which adult shad perish above the dam is not well understood. Studies conducted above Holyoke (Watson, 1968, 1970; Sherer, 1974; Foote, 1976) have demonstrated that adult mortality while ascending the fish lift ranged from 2.3 to 3.7 percent. Thus, substantial mortality probably occurred after spawning because of physiological exhaustion and because the fish were unable to descend from the Holyoke facility due to entrapment by the canal system.

For the linear regression equations, the Y- axis intercept (M_0) is interpreted as the estimate of natural mortality if no fish had passed over Holyoke. The (M_0) values were 0.2626 and 0.7439 for males and females, respectively, (see page 102 implying that natural mortality due to other factors (effects of the Holyoke dam held constant) is much greater among adult females. It is difficult to assess whether these extrapolated M_0 values approach the true mortality rates, or whether they are artifacts caused by random variation. Because age composition data have indicated that the shad is a relatively short-lived species which rarely exceeds age VIII, the female mortality rate (M_0) of 0.7439 appears reasonable, whereas the value 0.2626 for males is more likely a low estimate.

ESTIMATES OF RECRUITMENT

To complete the necessary information regarding the population parameters of adult shad, there remains the problem of determining the relative strength of the year classes which contribute to the annual run, 4, 5, and 6 years thereafter. The term "year class" refers to the year in which a particular generation is hatched. As an example, in 1960 an age IV female belonging to the 1956 year class would have deposited her eggs in the river sometime between late May and late June. Her surviving progeny, themselves belonging to the 1960 year class, would then return to the river and spawn between 1963 and 1966. By summing the numbers of virgin shad from year t + 3 through t + 6, then provides the total production of virgin recruits emanating from year class t.

Before continuing with this analysis, a distinction should be made between age at recruitment (t_r) to the adult population, and age at recruitment (t_c) to the fishery. The term (t_r) refers to the age at which the shad become sexually mature, leave the ocean, and ascend the Connecticut River to spawn for the first time. According to the spawning history data (Tables 9 and 10),most males reach t_r at ages III or IV, whereas females usually become sexually mature about one year later. Upon entry into the population, the virgin shad are liable to encounter the gill net fishery. However, due to the selective properties of the mesh sizes employed on the drift gill nets, many virgin shad are too small to be completely retained in the gear. As a result, these smaller fish remain for a time in what is called a pre-exploited phase. Eventually these fish grow and reach age t_c and length (L_c) in which they become fully vulnerable to capture, and thus are referred to as recruits to the fishery.

According to the 1976 and 1977 tagging studies (Tables 25 and 26), female shad are fully recruited to the gill net fishery at L_c of 49 or 50 cm which correspond to (t_c) of age V, though females ranging in length from 47 to 48 cm

Table 27. Mean ($\bar{x}$), standard deviation (s_x), and coefficient of variation (cv) for the proportion of virgin females from age group IV, V, and VI as determined by scale analysis, 1965 - 1977.

	Age group		
	IV	V	VI
Proportion of virgins/age group ($\bar{x}$)	0.1634	0.4846	0.0423
Standard deviation (s_x)	0.0554	0.1089	0.0213
Coefficient of variation (cv)	33.9%	22.5%	50.4%
Proportion of virgins/year class ($\bar{x}$)	23.7%	70.2%	6.1%

Table 28. Calculated numbers of virgin females produced by each year class from 1940 through 1971.

(1)	(2)	(3)	(4)	(5)	(6)
		Female progeny produced by age group			
Year	Female population	IV	V	VI	Total
1940	237,000	54,902	126,481	11,929	193,312
1941	365,500	42,647	136,657	8,883	188,187
1942	308,000	46,079	101,766	8,164	156,009
1943	331,000	34,314	93,528	6,662	134,504
1944	336,000	31,536	76,325	4,886	112,747
1945	261,000	25,736	55,971	6,599	88,306
1946	282,000	18,873	75,598	8,418	102,889
1947	210,000	25,490	96,435	6,578	128,503
1948	193,000	32,517	75,355	5,816	113,688
1949	157,500	25,409	66,633	4,547	96,589
1950	115,500	22,468	52,095	5,097	79,660
1951	156,000	17,566	58,394	8,568	84,528
1952	199,000	19,690	98,132	10,406	128,228
1953	155,500	33,089	119,212	10,046	163,347
1954	137,500	40,196	115,093	10,427	165,716
1955	107,500	38,808	119,454	10,406	168,668
1956	120,500	40,278	119,212	9,602	169,092
1957	202,500	40,196	110,004	6,853	157,053
1958	246,000	37,092	78,505	7,360	122,957
1959	237,500	26,471	84,320	8,460	119,251
1960	246,500	28,432	96,920	7,762	133,114
1961	246,000	32,680	88,924	7,783	129,387
1962	227,000	29,984	89,166	5,922	125,072
1963	162,000	30,066	67,844	7,043	104,953
1964	174,000	22,876	80,686	8,862	112,424
1965	200,000	27,206	101,524	9,052	137,782
1966	183,500	34,232	103,704	5,816	143,752
1967	184,000	34,968	66,633	7,022	108,623
1968	140,000	22,468	80,444	7,868	110,780
1969	166,500	27,124	90,136	10,660	127,920
1970	209,500	30,392	122,119	15,651	168,162
1971	214,000	41,177	179,302	6,831	227,310
1972	137,500	60,458	78,263		
1973	166,000				
1974	186,000				
1975	252,000				
1976	370,000				
1977	161,500				
	$\bar{x}$ =	32,588	94,086	8,124	134,454[1/]
	s =	9,743	26,494	2,292	33,841

1/ Average recruitment excluding the 1972 data approach full retention. In addition, these data suggest that age IV females (43 - 46 cm) are incompletely recruited to the fishery, since their fishing rates (u_c) were considerably less than those from larger fish. It is doubtful that adult males become completely liable to capture until about age VI (fork length 49 - 52 cm) due to their smaller length and girth; thus, few ever reach age t_c of full recruitment to the fishery.

Because each year's run is composed of virgin fish from an array of year classes, the average age composition (t_r) of virgin individuals must be discerned to extrapolate progeny production back to a particular escapement. As stated previously, due to the selective nature of the gill net fishery, the age composition and spawning history data for males are suspected to contain too many longer and older repeat spawners, so, this analysis will be confined to age data of females only.

The total number of female recruits produced by spawners in year t can be determined by summing the numbers of 4, 5, and 6 year old virgins in the total population during years t + 4, t + 5, and t + 6, respectively. From the spawning history data from 1965 - 1977, the average proportions of virgin females in age groups IV, V and VI are tabulated in Table 27. The total female progeny returning from a spawn in a given year (t) was then determined by employing the following expression:

$$P_t = 0.1634\ N_{t+4} + 0.4846\ N_{t+5} + 0.0423\ N_{t+6}$$

where P_t = total numbers of virgin females produced by year class t

$N_t + 4$ = estimated numbers of adult females in year t + 4

$N_t + 5$ = estimated numbers of adult females in year t + 5

$N_t + 6$ = estimated numbers of adult females in year t + 6

Estimated numbers of virgin females produced by each year class from 1940-1971 are assembled by age group in Columns 3, 4, and 5 of Table 28. The accuracy of these estimates is predicated upon two assumptions: 1) the proportion of 4, 5 and 6 year old virgins in the annual run is similar among years; and 2) the age composition and spawning history data for the period 1965 - 1977 are similar to those from earlier years (1940 - 1964). As for the first assumption, the coefficient of variation (CV) of age VI virgins is very high (50.4 percent); but since age VI virgins comprise only about 6.1 percent of the progeny/year class the loss in precision will be negligible (Table 27). In contrast, age IV and V females constitute 93.9 percent of the progeny/year class, and their (CV) values are much more acceptable at 33.9 and 22.5 percent, respectively. Annual variations in the proportion of 4, 5 and 6 year old virgins are primarily due to fluctuations in the year class recruitment, fishing mortality, and natural mortality. The second assumption appears to be satisfied as no great difference was noted between the age compositions of females presented here and those determined during the late 1950's (Nichols and Tagatz, 1960).

According to Column 6 Table 28, year class strength has varied during the period 1940 - 1971. For each year class, recruitment of males and females combined can be estimated by doubling female recruitment in column 6, Table 28. The data in column 6 suggest that dominant year classes occurred at approximately 15 year intervals: during 1940 and 1941; from 1953 - 1956; and during 1970 and 1971. Whether this 15 year cycle in year class strength is a coincidence, or whether it is the result of a real periodicity in survival from egg to first recruitment is not known.

Analyses concerning the relationships between female escapement and subsequent production, and between escapement and return per spawner are forthcoming in a following section of this report.

YIELD ASSESSMENT

The use of theoretical models is now an accepted technique for determining yield from an exploited fish population. Mathematical models have been developed by various authors (principally, Thompson and Bell, 1934; Ricker, 1945; Beverton and Holt, 1957) to demonstrate the theory of fishing in the computation of yield from a given number or recruits. In most instances the yields (weight of the catch) have been estimated at different rates of fishing by maintaining the parameters of growth, natural mortality, and recruitment at a constant. Results of these models are important in providing preliminary information regarding the changes in yield with corresponding changes in fishing effort. In addition, by manipulating the parameters of growth, natural mortality and recruitment, the model can then furnish a more realistic appraisal of either an increase or decrease in the present rate of fishing. The effects of fluctuations in the above parameters have been discussed by Dickie (1973), and complex simulation models taking into account non-equilibrium conditions have been developed by both Walters (1969) and Silliman (1969).

In this investigation, the model as derived by Thompson and Bell (1934) will be employed to estimate the following parameters at varying rates of fishing: 1) equilibrium size of the run; 2) equilibrium catch in numbers; 3) equilibrium yield in kg; 4) escapement to the spawning grounds; 5) proportion of repeat spawners; 6) average weight of a fish in the catch; and 7) annual fishing rate (u_{total}). Because this model was originally designed for a year-long fishery, some of the mathematical aspects had to be modified so as to conform with the seasonal nature of the commercial and sport fisheries. In this analysis the choice of the Thompson-Bell model was somewhat arbitrary since the models as derived by Ricker (1948) and Beverton and Holt (1957) would have served the purpose equally well. However, due to the versatility of the Thompson-Bell model, I felt that it was the easiest to apply.

In the previous sections, I have determined by sex the parameters of growth, mortality (fishing and natural) and recruitment. Because adult females are economically more valuable than males, and because the estimates of their vital parameters are suspected to be more reliable, only information relating to female shad will be applied to the yield model.

It has already been shown (Figure 1) that fluctuations in the commercial landings of adult shad from 1940 through 1977 are partly dependent upon changes in the fishing intensity as measured by the numbers of standard fishing unit days (SFU). According to the theory of fishing (Schaefer 1954; Beverton and Holt, 1957) this relationship between catch and fishing effort (SFU) is reflected by changes in the age composition upon which two factors have been instrumental in balancing the losses in stock biomass from fishing and natural causes. They are: 1) increases in weight of the stock due to growth of the surviving individuals; and 2) additions in weight due to recruitment from incoming year classes. Moreover, each increase in fishing mortality results in a series of characteristic reactions to the age structure of the population which are quite unrelated to alterations in recruitment. For example, in a less intense fishery, more adult shad are allowed to survive into the older age groups because total mortality is lower than in a more intense fishery. As a consequence, if increments in weight due to growth exceeds the loss in numbers from natural mortality, the less intense fishery not only produces a greater yield per unit of fishing effort, but also a greater total annual yield. Thus, the level of fishing which would produce a maximum sustainable yield from a fish population is dependent on the rates of growth and natural mortality.

In this section a number of theoretical tenets will be presented regarding the shad's age structure and spawning history, the principals of which are generally recognized in the study of fish population dynamics. Three aspects of the model will be compared among different fishing rates: the proportion of repeat spawners, the yield in kg, and the average weight of a female in the catch. When the age composition of the population is considered, alterations in the rates of natural mortality and fishing mortality produce changes in the numbers of older fish. I shall show that the yields, proportion of repeat spawners, and average weight of a female which have occurred in the actual statistics from 1966 - 1974, are similar to the predicted values from the yield model.

The fundamental assumption implicit with the Thompson - Bell model as with all models of this type is that the shad population remains in a state of dynamic equilibrium. According to Ricker (1975), equilibrium conditions are approached whenever fishing mortality is sufficiently constant during a long enough period as to affect a year class throughout its exploitable life. The condition of equilibrium is synonomous to the "steady state" as interpreted by Beverton and Holt (1957, p. 37); _ _ _ _ _"when a population or a fishery is not in the process of changing either in character or size; the term allows for the existence of fluctuations with a periodicity of one year, and also for the year to year variations caused by fluctuations in factors such as the annual recruitment (which for the shad will certainly occur), provided they are not excessive".

Thus an equilibrium is here understood to mean a condition in which the weight of fish removed by fishing and natural causes is on the average equivalent to the weight added through growth and recruitment. Under steady-state conditions, the yield from a single year class throughout its fishable life is equivalent to the yield from all year classes present during a single year. In simple terms, a female shad can either be captured by the fisheries, lost to natural causes, or survive to the next year. The numbers of fish that die can be estimated as funtions of both fishing (F) and natural (M) mortalities, and the yields in weight taken during the fishing season will be synonomous to the product of the catches in numbers times the average weights. Therefore, the population is influenced by alterations in the rates of growth, natural mortality, and recruitment rather than as merely a series of increments and decrements in weight or numbers. Having estimated growth and natural mortality, the female shad population can be theoretically reconstructed by age group and total yields can then be computed at various levels of fishing mortality.

For any fish population, equilibrium conditions are only a reality during short periods of a fishery, since neither total mortality nor recruitment are likely to remain constant for very long periods. As for the shad, the assumption of steady-state conditions during the period 1940 - 1977 is unrealistic because total mortality has varied considerably, being high during the mid 1940's due to heavy fishing pressure and progressively declining thereafter (Figure 1). In addition long-term andpersistent fluctuations in virgin recruitment have occurred which further dispells the steady-state condition (Table 28). However, during the period 1966 - 1974 both total mortality and recruitment have been essentially constant, so that this period of the fishery appears to approach a steady-state condition. Certain statistics from the actual fishery (1966 - 1974) will be compared to the equilibrium values as computed from the model to determine whether the predicted values approximate those from the actual fishery.

The application of the Thompson-Bell model requires the fulfillment of specific assumptions relating to steady-state conditions. The validity of the results depend upon the degree to which the following conditions are satisfied: 1) natural mortality is constant from the age of recruitment to the end of the fishable lifespan; 2) natural mortality occurs during a time of year other than the fishing season; 3) the growth rate (length and weight) follows the von Bertalanffy expression and is age-specific but density-independent; 4) virgin recruitment is constant and unaffected by the size of the parent stock; and 5) age IV females are incompletely retained in the gill nets, and thus are subjected to a fishing mortality rate (F) that is 33 percent less than that for successive age groups.

As for the first assumption, it is not known whether natural mortality increases with age, though it is strongly suspected. Accordingly, the model will be modified later to include age-specific natural mortality. Regarding assumption 2, nothing is known of the seasonal pattern of natural mortality among adult females, and it may be unrealistic to assume that no natural mortality occurs during the fishing season. Nevertheless a fish cannot be lost to both fishing and natural causes, and because the fishing effort is sufficiently intense during April and May, natural mortality during this period is expected to be minimal. Assumption 3 is believed to be valid since the calculated length and weight by age group as derived from the von Bertalanffy equation agreed well with the observed data. Though some researchers have provided evidence that density-dependent growth occurs during the adult phase (Anthony, 1971), most studies have shown that compensatory growth is relegated to the early life-history stages (Beverton and Holt, 1957 ; Beverton, 1962; Cushing, 1977). As a result, density-independent growth of adult shad is a plausible assumption. The assumption that virgin recruitment is constant and independent of parent stock may be approximately true only for low and intermediate rates of fishing (u_{total} of 10 to 50 percent). For annual rates of fishing (u_{total}) greater than 50 percent, the numbers of females escaping to the spawning grounds may be unable to produce enough replacements in the filial generation. Hence, the size of the shad run under intense exploitation would inevitably decline in successive generations resulting in a concomitant reduction in yield and in yield per unit effort to the sport and commercial fisheries. In the following section, the stock-recruitment relationship will be estimated, and from this relationship a more complex but realistic model will be developed which considers variations in yield with corresponding changes in the size of the parent stock. Assumption 5 regarding age specific fishing mortality appears sound since according to the mark-recapture data from 1976 - 1977 (Tables 25 and 26), most age IV females (fork length of 42 - 47 cm) are incompletely retained by the drift gill nets.

Using the Thompson-Bell model, equilibrium yield (Y) in year (t) from the commercial and sport fisheries combined is given by

$$Y_t = \sum_{r \text{ to } v} (R_{xt} + A_{xt})\, u_{xt} \bar{w}_{xt}, \qquad (27)$$

where: R_{xt} = numbers of virgin females of age group (x) in year (t)

A_{xt} = numbers of repeat spawning females of age group (x) in year (t)

u_{xt} = annual fishing rate of age group (x) in year (t)

$\bar{w}_{xt}$ = average weight (kg) of age group (x) in year (t)

r = age at first recruitment (i.e. age IV female shad)

v = greatest age attainable (i.e. age XI female shad).

From the above expression, equilibrium size of the female run (B_t) is equivalent to

$$\sum_{r \text{ to } v} R_{xt} + A_{xt},$$

and the equilibrium catch (C_t) in numbers is expressed by

$$B_t u_t,$$

where u_t = annual fishing rate due to commercial and sport fishing in year (t).

The percent repeat spawners (H_t) is expressed by

$$\sum_{r \text{ to } v} A_{xt}/B_t,$$

Table 29. Computation for the Thompson-Bell yield model when 40,000 age IV, 90,000 age V and 9,000 age VI virgin females enter the fishery.

(1) Age group	(2) Virgin recruitment	(3) Repeat spawners	(4) Total run	(5) Catch in numbers	(6) Average weight (kg)	(7) Yield (kg)
IV	40,000	-	40,000	7,280	1.606	11,692
V	90,000	14,716	104,716	27,121	2.032	55,110
VI	9,000	34,860	43,860	11,360	2.435	27,662
VII	-	14,601	14,601	3,782	2.805	10,609
VIII	-	4,861	4,861	1,259	3.137	3,949
IX	-	1,618	1,618	419	3.429	1,437
X	-	539	539	140	3.683	516
XI	-	179	179	46	3.901	179
Sum of columns		71,374	210,374	51,407		111,154

Parameters used in the model

	Age IV		All successive age groups
F_{total}	0.20	F_{total}	0.30
u_{total}	18.2%	u_{total}	25.9%
M	0.8	M	0.8
Z	1.00	Z	1.10
S	36.79%	S	33.29%

Computed parameters

(1) Female run	(2) Repeat spawners	(3) Catch	(4) Yield	(5) %Repeat	(6) u_{total}	(7) Av. weight	(8) Escapem
210,374	71,374	51,407	111,154	34.0	24.4%	2.162	158,96

and the average weight (kg) of a female shad (W_t) in the catch is obtained by the component

Y_t/C_t.

Equilibrium escapement (P_t) of female shad to the spawning grounds is expressed by

$B_t - C_t$

Table 29 provides an example of the computation where 40,000 age IV, 90,000 age V, and 9,000 age VI virgin female shad from three successive year classes simultaneously enter the Connecticut River. This level of annual virgin recruitment is similar to the average numbers which entered the river from 1940 - 1971 (Table 28). Age IV fish are subjected to an annual fishing rate (u_{total}) of 18.2 percent, whereas fish from age V - XI are considered fully vulnerable to the gear and are taken at a rate of 25.9 percent. The corresponding instantaneous rates (F_{total}) of 0.20 and 0.30, respectively, are determined by using the expression:

$$F = -\ln(1 - u_{total}).$$

These levels of fishing mortality (F_{total}) are chosen because they approach the actual values during the period 1966 - 1974 (Column 6, Table 22). All age groups sustain losses due to natural causes at an instantaneous rate (M) of 0.8 which again is typical of the period 1966 - 1974 (Column 3 Table 23). Instantaneous rates of total mortality (Z) are determined as 1.00 for age IV fish and 1.10 for all age groups thereafter using the expression:

$$Z = F_{total} + M.$$

Annual survival rates (S) were computed as 36.79 percent for fish of age IV and 33.29 percent for fish of ages V - XI by employing the following equation:

$$S = e^{-Z}$$

Age-specific weight (kg) are shown in Column 6 Table 29 and were derived previously from the von Bertalanffy equation

$$W_x = W_\infty\left[1 - e^{-K(t - t_0)}\right]^n .$$

The computation of the model proceeds as follows: the 40,000 age IV females (Column 2 Table 29) are subjected to an annual fishing rate of 18.2 percent; this yields 7280 individuals (Column 5). The yield 11,692 kg (Column 7) is obtained by multiplying the catch (7280) by the average weight (1.606 kg) at age IV (Column 6). Of the 40,000 age IV females, 36.79 percent or 14716 individuals survive and recur as age V repeat spawners (Column 3). These repeat spawners are joined by 90,000 age V virgins (Column 2) resulting in a total number of 104716 age V females (Column 4). These age fish are then exploited by an annual fishing rate of 25.9 percent resulting in a catch of 27121 individuals (Column 5). The yield of 55110 kg (Column 7) is determined by the product of the average weight (Column 6) and the catch in numbers (Column 5). Of the 104716 age V females, 33.29 percent or 34860 survive and recur as age VI repeat spawners (Column 3). These repeat spawners are joined by 9000 age VI virgins resulting in 43860 age VI individuals (Column 4). The above calculations are repeated for each age group up to and including age XI. The sum of Columns 3, 4, 5 and 7, respectively, provides equilibrium estimates of the following parameters: numbers of repeat spawners, size of the female population, catch in numbers, and yield in kg. From these data, additional parameters can be computed as follows: percent repeat spawners, annual rate of fishing (u_{total}). average weight per female, and the numbers of females escaping to the spawning grounds.

Eight vital parameters emperically determined are shown in the bottom row of Table 29. Under the prescribed conditions, equilibrium size of the female run is 210,374 individuals (sum of Column 4 Table 29), 71374 of which are repeat spawners (sum of Column 3). Assuming a 50:50 sex ratio, the total run (male and females combined) is estimated as 420,748 by doubling the female population. The equilibrium

Table 30. Various statistics from the actual fishery, 1966 - 1974, and a comparison between the observed and predicted statistics.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Year	Size of female run	Commercial and sport catch in numbers[1/]	Annual fishing rate u_{total}[2/]	Av.weight of female (kg)[3/]	Yield(kg) in weight	Percent of repeat spawners[4/]	Numbers of repeats	Escapement
1966	183,500	62,813	34.2	1.829	114,885	51.0	93,585	120,687
1967	184,000	51,295	27.9	1.887	96,794	46.0	84,640	132,705
1968	140,000	40,163	28.7	1.935	77,715	23.0	32,200	99,837
1969	166,500	51,742	31.1	1.863	96,395	30.0	49,950	114,758
1970	209,500	49,501	23.6	-	-	33.0	69,135	159,999
1971	214,000	53,893	25.2	-	-	27.0	57,780	160,107
1972	137,500	34,647	25.2	2.113	73,209	27.0	37,125	102,853
1973	166,000	47,512	28.6	2.180	103,576	46.0	76,360	118,488
1974	186,000	45,747	24.6	2.250	102.931	31.8	59,148	140,253
Mean value	176,333	48,590	27.8	2.008	95,072	35.0	62,214	127,743
Standard dev.	26,819	8,087	3.4	0.169	14,780	10.1	20,751	22,280
				Expected values				
Mean	210,374	51,407	24.4	2.162	111,154	34.0	71,374	158,967
			Percent difference between computed and expected					
% Difference	-16.2	-515	+13.9	- 7.1	-14.5	-2.9	-12.9	-19.6

Av. difference - 8.1%

Standard deviation 10.6%

continued

Table 30 Continued

1/ Commercial landings were adjusted by Chi square analysis

2/ u_{total} = catch in numbers/size of female run

3/ Av. weight (kg) = yield (kg)/catch in numbers

4/ Percent of repeat spawners were from Leggett (1976, Table 128, p. 206)

Table 31. A comparison between the age composition and spawning history of female shad from the actual fishery, 1966 - 1974, and those derived from the Thompson-Bell model.

Actual[1/]								
Age	IV	V	VI	VII	VIII	IX	X	XI
% age composition	16.5	49.4	23.0	7.6	2.8	0.6	0.1	-
% repeat spawners	0.0	13.0	79.2	97.8	100.0	100.0	100.0	-
% virgin spawners	100.0	87.0	20.8	2.2	0.0	0.0	0.0	-

Projected[2/]								
Age	IV	V	VI	VII	VIII	IX	X	XI
Numbers	40,000	104,716	43,860	14,601	4,861	1618	539	179
% age composition	19.0	49.8	20.8	6.9	2.3	0.8	0.3	0.1
% repeat spawners	0.0	14.1	79.5	100.0	100.0	100.0	100.0	100.0
% virgin spawners	100.0	85.9	20.5	0.0	0.0	0.0	0.0	0.0

[1/] Age composition and spawning history 1966 - 1973 taken from Leggett (1976, Tables 126, and 129).

[2/] Age composition and spawning history were determined from columns 3 and 4, Table 29.

catch in numbers is 51407 female shad (sum of column 5), and the equilibrium yield is 111,154 kg (sum of Column 7). The percent repeat spawners is estimated as 34.0 percent by dividing the numbers of repeat spawners (71374) by the size of the female run (210,374). The annual fishing mortality of 24.4 percent is computed by dividing the catch (51407) by the size of the run (210,374). Average weight of a female shad in the catch (2.162 kg) is resolved by dividing the yield in weight (111,154 kg) by the catch (51407) in numbers. Escapement of females (158,967) to the spawning grounds is determined by subtracting the catch (51407) from the run of females (210,374).

The predicted parameters are compared to those from the actual fishery from 1966 - 1974 in Table 30. The observed and expected parameters are strikingly similar, the actual values being on the average 8.1 percent lower than the predicted values. Thus,the yield model appears to explain much of the changes which have occurred in the fishery from 1966 through 1974. The theoretical age composition and spawning history computed from Columns 3 and 4 of Table 29 are also shown with the average values from 1966 - 1974 (Table 31). The theoretical age structure is very similar to that determined from scale analysis for the period 1966-1974. This suggest that the levels of fishing (F) and natural mortality (M) chosen for the model realistically reflect the reduction in numbers of the shad population.

The results of the above example demonstrate that the proposed yield model provides estimates of key parameters which are recognizable in the actual statistics. There is little doubt but that the theory behind this model corresponds sufficiently to the actual processes occurring in the adult shad population, and that the model will reflect the transitory effects of fishing upon the shad population. The small dissimilarity observed between actual and predicted values was certainly expected since the actual parameters of growth, natural mortality, and recruitment vary annually due to many factors which are not yet fully understood. Moreover, the manner in which these factors influence a natural population is unlikely to be as simple as that applied in the present model.

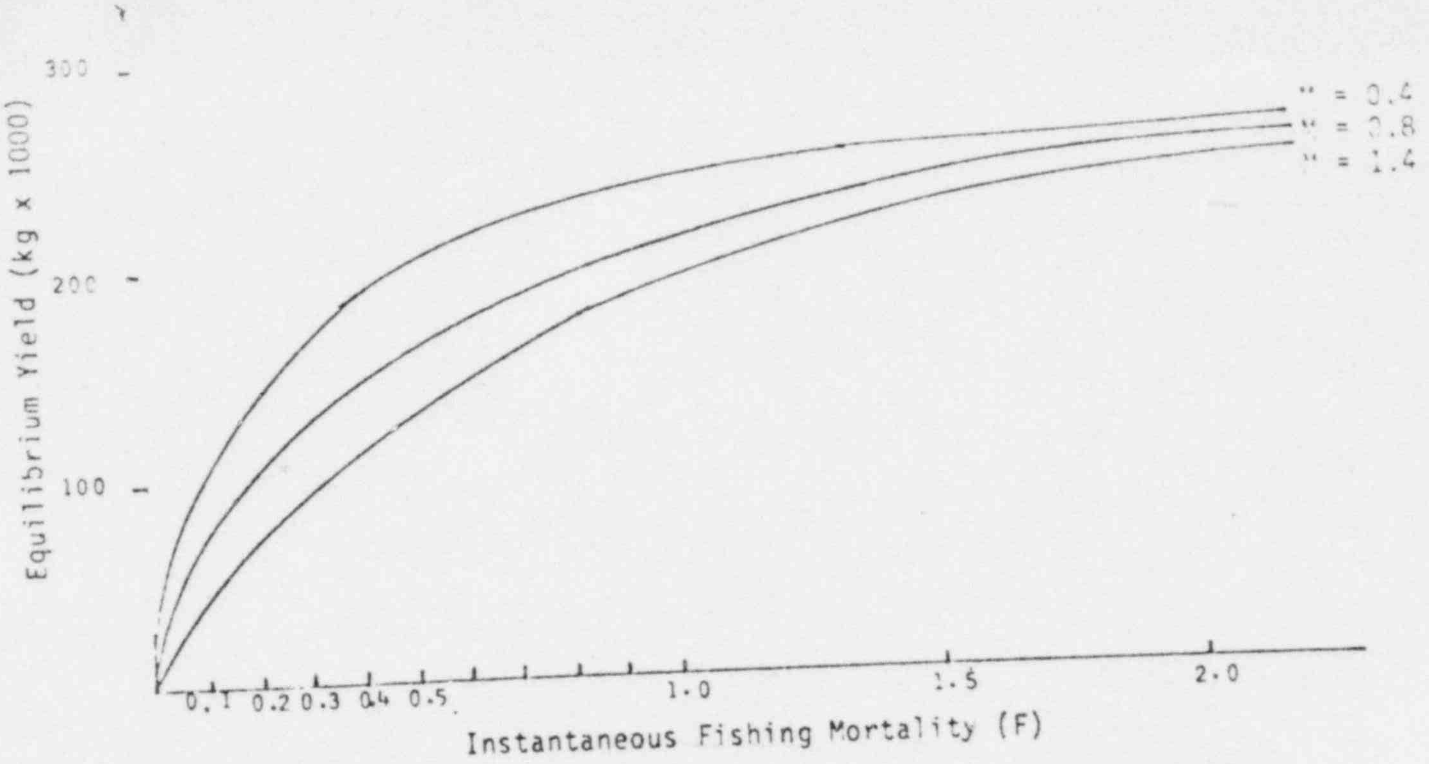

Figure 12. Equilibrium yield (kg) at various combinations of fishing (F) and natural mortalities (M constant for age group IV through XI).

Table 32. Estimates of yield[1/] and other parameters using the Thompson-Bell model at various fishing rates with natural mortality held constant ($M = 0.4$).

(1) F_{total}	(2) u_{total}	(3) Fishing effort (SFU)	(4) Size of female run	(5) Catch in numbers	(6) Escapement	(7) % repeat spawners	(8) Yield kg	(9) Av weight per female (kg)	(10) Yield/ effort	(11) Yield/ yield max	(12) Yield efficiency
0.09	9%	411	345,200	31,600	313,600	60.9	77,800	2.462	189	0.293	55.38
0.19	17%	868	307,300	53,400	253,900	58.3	127,400	2.386	147	0.480	70.56
0.27	24%	1,233	278,400	69,000	209,400	50.4	160,300	2.323	130	0.604	78.52 **
0.37	31%	1,689	256,100	80,700	175,400	45.9	183,200	2.270	108	0.690	74.52 **
0.46	37%	2,100	238,600	89,600	149,000	41.8	199,300	2.224	95	0.751	71.35
0.69	50%	3,151	208,600	104,700	103,900	33.4	224,700	2.146	71	0.847	60.14
0.92	60%	4,201	189,600	114,100	75,500	26.7	238,500	2.090	57	0.899	51.24
1.14	68%	5,205	176,800	120,400	56,400	21.4	247,300	2.054	48	0.932	44.74
1.35	74%	6,164	167,900	124,800	43,100	17.2	253,000	2.027	41	0.953	39.07
1.77	83%	8,082	156,600	130,400	26,200	11.2	259,800	1.992	32	0.979	31.33
2.21	89%	10,091	150,000	133,600	16,400	7.4	263,400	1.972	26	0.992	25.79
2.66	93%	12,146	146,100	135,500	10,600	4.9	265,400	1.959	22	1.000	22.00

[1/] Values rounded to the nearest hundred

** denotes the fishing rates which produce an optimium yield per SFU

Table 33. Estimates of yield[1/] and other parameters using the Thompson-Bell model at various fishing rates with natural mortality held constant (M = 0.8)

(1) F_{total}	(2) u_{total}	(3) Fishing effort (SFU)	(4) Size of female run	(5) Catch in numbers	(6) Escapement	(7) % repeat spawners	(8) Yield kg	(9) Av weight per female (kg)	(10) Yield/ effort	(11) Yield/ yield max	(12) Yield efficien
0.09	9%	411	234,700	21,100	213,600	40.9	47,000	2.227	114	0.181	20.63
0.19	17%	868	221,400	37,800	183,600	37.3	83,000	2.196	96	0.320	30.72
0.27	24%	1,233	210,400	51,400	159,000	34.0	111,200	2.163	90	0.429	38.61
0.37	31%	1,689	201,300	62,600	138.700	31.1	133,700	2.136	79	0.516	40.76
0.46	37%	2,100	193,700	71,800	121,900	28.2	151,700	2.113	72	0.585	42.12 *
0.69	50%	3,151	179,500	89,400	90,100	22.6	185,100	2.070	59	0.714	42.13 *
0.92	60%	4,201	169,600	101,400	68,200	18.1	206,900	2.040	49	0.799	39.15
1.14	68%	5,205	162,500	110,000	52,500	14.5	222,000	2.018	43	0.857	36.85
1.35	74%	6,164	157,300	116,600	40,700	11.6	233,200	2.000	38	0.900	34.20
1.77	83%	8,082	150,400	125,000	25,400	7.6	247,300	1.978	31	0.954	29.57
2.21	89%	10,091	146,300	130,100	16,200	5.0	255,500	1.964	25	0.986	24.65
2.66	93%	12,146	143,100	132,600	10,500	2.9	259,100	1.954	21	1.000	21.00

[1/] Values rounded to the nearest hundred

** denotes the fishing rates which produce an optimium yield per SFU

Table 34. Estimate of yield[1/] and other parameters using the Thompson-Bell model at various fishing rates with natural mortality held constant (M = 1.4).

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
F_{total}	u_{total}	Fishing effort (SFU)	Size of female run	Catch in numbers	Escapement	% repeat spawners	Yield kg	Av weight per female (kg)	Yield/ effort	Yield/ yield max.	Yield efficiency
0.09	9%	411	179,300	15,800	163,500	22.5	33,000	2.089	80	0.129	10.32
0.19	17%	868	174,900	29,400	145,500	20.5	60,900	2.071	70	0.238	16.66
0.27	24%	1,233	171,000	41,200	129,800	18.7	84,700	2.056	69	0.331	22.84
0.37	31%	1,689	167,620	51,600	116,020	17.1	105,500	2.045	62	0.413	25.61
0.46	37%	2,100	164,700	60,500	104,200	15.6	123,100	2.035	59	0.481	28.38
0.69	50%	3,151	158,800	78,500	80,300	12.5	158,200	2.015	50	0.619	30.95 **
0.92	60%	4,201	154,400	91,800	62,600	10.0	183,700	2.001	44	0.718	31.59 **
1.14	68%	5,205	151,100	102,000	49,100	8.0	202,700	1.987	39	0.793	30.93 **
1.35	74%	6,164	148,600	109,800	38,800	6.4	217,200	1.978	35	0.849	29.72
1.77	83%	8,082	145,100	120,400	24,700	4.2	236,600	1.965	29	0.925	26.83
2.21	89%	10,091	142,900	127,000	15,900	2.7	248,500	1.957	25	0.972	24.30
2.66	93%	12,146	141,600	131,100	10,500	1.8	255,700	1.950	21	1.000	21.00

[1/] Values rounded to the nearest hundred

** denot[illegible] the fishing rates which produce an optimum yiel[illegible] r SFU

The eight parameters previously described were estimated using the model at three levels of natural mortality (M = 0.4, 0.8, 1.4), each in combination with various rates of fishing mortality (F from 0.09 to 2.66). An M of 0.4 was chosen for comparative purposes to determine the relationship between yield and a decline in natural mortality. An M of 0.8 was selected because it was typical of the level which actually occurred from 1966 through 1974, whereas an M of 1.4 approaches the level which occurred concurrent with substantial spawning in the Holyoke pool during the period 1975 - 1977. The model was employed to determine equilibrium yields from the commercial and sport fisheries combined. Although it may be more realistic to determine yield from each fishery separately, a model specifically concerned with the sport fishery would be difficult to develop, since accurate information relating to the selective properties of the sport fishery is presently unavailable. For the present purposes, size selectivity of the sport fishery was assumed similiar to that of the commercial fishery. Futher details regarding the model are presented in ppendix 1.

Because the assumption regarding constant natural mortality (M) may be suspect, two possibilities were explored concerning the trend in natural mortality with age. These are: Case 1, where natural mortality (M) is constant for all age groups; and Case 2, where M is constant for ages IV through VI, and then it is allowed to increase by 25 percent for each age group thereafter.

Results

(a) Case 1 - constant natural mortality (M)

Results of the analysis under the prescribed conditions are shown in Tables 32-34. The relationship between yield in kg and fishing mortality (F) at the three levels of natural mortality (M) are graphically portrayed in Figure 12. According to Tables 32 - 34, the pro- rtion of repeat spawners (Column 7), catch in numbers (Column 5), average weight of an individual fish (Column 9), and total yield (Column 8) are always greatest at the low rate of mortality (0.4). This occurs because at an M of 0.4, more female shad are able to survive and grow into the older age groups. However, at high rates of fishing (F = 0.92 to 2.66), the yields (Figure 12) tend to converge regardless of natural mortality.

The fishing effort in standard fishing units (SFU) was determined for each level of fishing mortality (F_{total}) examined (Column 1, Tables 32-34) by assuming that the best nominal units of fishing effort are proportional to fishing mortality such that:

$F = pn$

where p = catchability coefficient (constant)

n = total fishing effort (SFU).

In a previous section (see page 29), the average catchability coefficient ($\bar{p}$) was estimated as 0.000175 for both sexes combined. However, because this analysis deals only with female shad, and because females are subjected to a higher rate of fishing mortality than are males, the catchability coefficient ($\bar{p}$) was recalculated so as to conform with the female fishing mortality (F). According to Column 1 of Table 24, average F_c values for males and females is 0.1624 and 0.2722, respectively, resulting in an F_c value of 0.2173 for both sexes combined. The catchability coefficient (0.000219) for females was then estimated using the following expression:

$(0.2722)\ (0.000175)/0.2173 = 0.000219$

The estimates of fishing effort (Column 3 Tables 32-34) were computed by dividing the F values (Column 1) by the catchability coefficient (0.000219). Of course, the catchability coefficient (0.000219) computed here pertains only to the commercial fishery, so that it is somewhat unrealistic to use this value for determining effort for both fisheries. Nevertheless, because a catchability coefficient is presently unattainable for the sport fishery, and because the sport catch comprises only about 10 percent of the total annual catch, I felt for simplicity and without undue error that the value 0.000219 can be employed to determine relative effort for both fisheries.

For any species, the shape of the yield curve will vary depending upon the estimated rates of growth (K of von Bertalanffy) and natural mortality (M). When natural mortality (M) exceeds growth (K), the curve relating yield to fishing mortality (F) is asymptotic in which above fairly low levels of fishing, further increases in F produce only marginal gains in yield. Conversely, when growth (K) exceeds natural mortality (M), the yield curve is dome-shaped with a well defined maximum yield at low levels of fishing. Because the natural mortality rates employed here (M = 0.4, 0.8, 1.4) are considerably greater than the computed growth rate (K = 0.1937), the three yield curves (Figure 12) are asymptotic without a clearly defined maximum. As a result, maximum sustainable yield cannot be determined directly from the yield curve. In fact, the asymptotic shape of the curves gives the superficial impression that fishing mortality (F) can be increased to high levels without any reduction in equilibrium yield. Yet such an interpretation would be not only erroneous, but also dangerous to the very survival of the shad population because the assumption that virgin recruitment is independent of parent stock may be invalid at high fishing rates. For example, at an M of 0.8 (Table 33), if annual fishing mortality (u_{total}) was increased to 74 percent (Column 2), only about 40,700 females (Column 6) would escape to spawn annually. It is doubtful that 40,700 females could produce enough progeny to sustain the total yield (Column 8) and the yield per effort (Column 10) at the predicted levels.

Due to the inherent limitations of the model, a yield efficiency coefficient was determined in lieu of the maximum sustainable yield. The highest value (as denoted by double asterisks in Column 12, Tables 32 - 34) is defined as the optimum yield per expenditure of fishing effort (SFU). It is computed by multiplying the yield (kg) per effort (Column 10) times the ratio of the equilibrium yield to the maximum yield (Column 11). Although certain authors (principally, Christy and Scott, 1965) have suggested that the optimum yield should be based on the maximum net economic yield (the difference between the economic and social value of the catch and the cost of catching it), a strict economic definition has its own disadvantages because the net economic yield will depend upon the market price of the fish and the cost of fishing which is known to vary within and among years. Thus, a strict economic definition for optimum yield fails to provide a fixed reference point for determining an appropriate level of fishing effort.

At an M of 0.4, optimal yields are obtained at rates of fishing (F) ranging from 0.27 to 0.37; these correspond to fishing efforts ranging from 1233 to 1689 SFU (Column 12, Table 32). At an M of 0.8, optimal yields occur at (F) ranging from 0.46 to 0.69 (Table 33). But at the highest rate of natural mortality (1.4) examined (Table 34), optimum yields are attained at much higher rates of fishing (0.69 to 1.14). This occurs because fewer female shad survive into the older age groups (ages VII - VIII) due to high natural mortality. Thus from the commercial fishermen's standpoint, it is more profitable to expend more effort in the fishery when natural mortality is high. Yet from a management standpoint, these high rates of fishing (F = 0.69 to 1.14) may reduce the parent stock to dangerously low levels. Thus under conditions of high natural mortality (M of 1.4 or greater), fishing effort should be restrained below the levels which produce an optimal yield to ensure an adequate female stock. Maintaining effort (SFU) at levels no higher than 1233 SFU allows 129,800 females (Column 6, Table 34) to spawn annually and would be consistent with the above management strategy.

According to Tables 32 - 34 and Figure 12, as natural mortality (M) increases, equilibrium yield to both fisheries declines regardless of the fishing rate (F). Furthermore, at the present rate of fishing (F = 0.27), when natural mortality (M) increases from 0.8 to 1.4 (Column 8, Tables 33 and 34), equilibrium yield declines from 111,200 kg to 84,700 kg (a 23 percent decline). These reductions in long-term yield should occur as a result of the following alterations in the shad population: 1) decline in the percent of repeat spawners from 34.0 percent to below 19 percent (Column 7, Tables 33 and 34); 2) decrease in the average weight (kg) of a female shad from 2.163 kg to 2.056 kg (Column 9, Tables 33 and 34); 3) reduction in the

Table 35. Estimates of yield$^{1/}$ and other parameters using the Thompson-Bell model at various fishing rates with natural mortality increasing by 25 percent for age VII females and onward ($M = 0.4$).

(1) F_{total}	(2) u_{total}	(3) Fishing effort (SFU)	(4) Size of female run	(5) Catch in numbers	(6) Escapement	(7) % repeat spawners	(8) Yield kg	(9) Av. weight per female (kg)	(10) Yield/ effort	(11) Yield/ yield max.	(12) Optimal efficiency
0.09	9%	411	327,700	30,000	297,700	57.7	71,800	2.393	175	0.270	47.25
0.19	17%	868	296,200	51,300	244,900	53.4	120,100	2.341	138	0.452	62.38
0.27	24%	1,233	271,200	67,100	204,100	48.8	153,800	2.292	125	0.579	72.38**
0.37	31%	1,689	251,500	79,300	172,200	44.8	178,100	2.246	105	0.671	70.46**
0.46	37%	2,100	235,900	88,200	147,700	41.1	195,000	2.211	93	0.734	68.26
0.69	50%	3,151	207,500	104,200	103,300	33.0	222,800	2.138	71	0.839	59.57
0.92	60%	4,201	189,200	113,800	75,400	26.5	237,600	2.008	57	0.895	51.02
1.14	68%	5,205	176,800	120,200	56,600	21.4	246,600	2.052	47	0.929	43.66
1.35	74%	6,164	168,000	124,700	43,300	17.2	252,700	2.026	41	0.952	39.03
1.77	83%	8,082	156,700	130,300	26,400	11.3	259,800	1.994	32	0.979	31.33
2.21	89%	10,091	150,100	133,500	16,600	7.4	263,400	1.973	26	0.992	25.79
2.66	93%	12,146	146,200	135,500	10,700	4.9	265,500	1.959	22	1.000	22.00

1/ Values rounded to the nearest hundred.

** denotes the fishing rates which produce an optimum yield per SFU

Table 36. Estimates of yield[1/] and other parameters using the Thompson-Bell model at various fishing rates with natural mortality increasing by 25 percent for age VII females and onward (M = 0.8).

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
F_{total}	u_{total}	Fishing effort (SFU)	Size of female run	Catch in numbers	Escapement	% repeat spawners	Yield kg	Av. weight per female (kg)	Yield/ effort	Yield/ yield max.	Optim effic
0.09	9%	411	229,900	20,700	209,200	39.5	45,600	2.203	111	0.175	19.43
0.19	17%	868	218,200	37,100	181,100	36.3	80,800	2.178	93	0.310	28.83
0.27	24%	1,233	208,100	50,800	157,300	33.2	109,100	2.148	88	0.419	36.87
0.37	31%	1,689	199,700	62,200	137,500	30.4	132,200	2.125	78	0.508	39.62
0.46	37%	2,100	192,800	71,300	121,500	27.9	150,203	2.107	71	0.577	40.97
0.69	50%	3,151	179,100	89,100	90,000	22.4	184,300	2.068	58	0.708	41.06
0.92	60%	4,201	169,400	101,300	68,100	18.0	206,500	2.038	49	0.793	38.86
1.14	68%	5,205	162,500	110,000	52,500	14.5	221,800	2.016	43	0.852	36.64
1.35	74%	6,164	157,300	116,500	40,800	11.7	233,000	2.000	38	0.895	34.01
1.77	83%	8,082	150,500	125,000	25,500	7.6	247,200	1.978	31	0.950	29.45
2.21	89%	10,091	146,300	130,100	16,200	5.0	255,400	1.963	25	0.981	24.53
2.66	93%	12,146	143,800	133,200	10,600	3.3	260,300	1.954	21	1.000	21.00

1/ Values rounded to the nearest hundred

** denotes the fishing rates which produce an optimum yield per SFU

Table 37. Estimates of yield[1/] and other parameters using the Thompson-Bell model at various fishing rates with natural mortality increasing by 25 percent for age VII females and onward (M = 1.4).

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
F_{total}	u_{total}	Fishing effort (SFU)	Size of female run	Catch in numbers	Escapement	% repeat spawners	Yield kg	Av.weight per female (kg)	Yield/ effort	Yield/ yield max.	Optimal efficiency
0.09	9%	411	178,500	15,800	162,700	22.1	32,700	2.070	80	0.128	10.24
0.19	17%	868	174,300	29,200	145,100	20.3	60,400	2.068	70	0.236	16.52
0.27	24%	1,233	170,600	41,100	129,500	18.5	84,400	2.054	68	0.330	22.44
0.37	31%	1,689	167,300	51,500	115,800	16.9	105,200	2.043	62	0.412	25.54
0.46	37%	2.100	164,500	60,200	104,300	15.5	122,500	2.035	58	0.479	27.78
0.69	50%	3,151	158,700	78,400	80,300	12.4	158,000	2.015	50	0.618	30.90**
0.92	60%	4,201	154,400	91 800	62,600	10.0	183,600	2.000	44	0.718	31.59**
1.14	68%	5,205	151,100	101,900	49,200	8.0	202,500	1.987	39	0.792	30.89**
1.35	74%	6,164	148,600	109,700	38,900	6.5	217,000	1.978	35	0.849	29.72
1.77	83%	8,082	145,000	120,300	24,700	4.2	236,400	1.965	29	0.425	26.83
2.21	89%	10,091	143,000	127,000	16,000	2.8	248,300	1.955	25	0.971	24.28
2.66	93%	12,146	141,600	131,100	10,400	1.8	255,600	1.950	21	1.000	21.00

1/ Values rounded to the nearest hundred

** denotes the fishing rates which produce an optimum yield per SFU

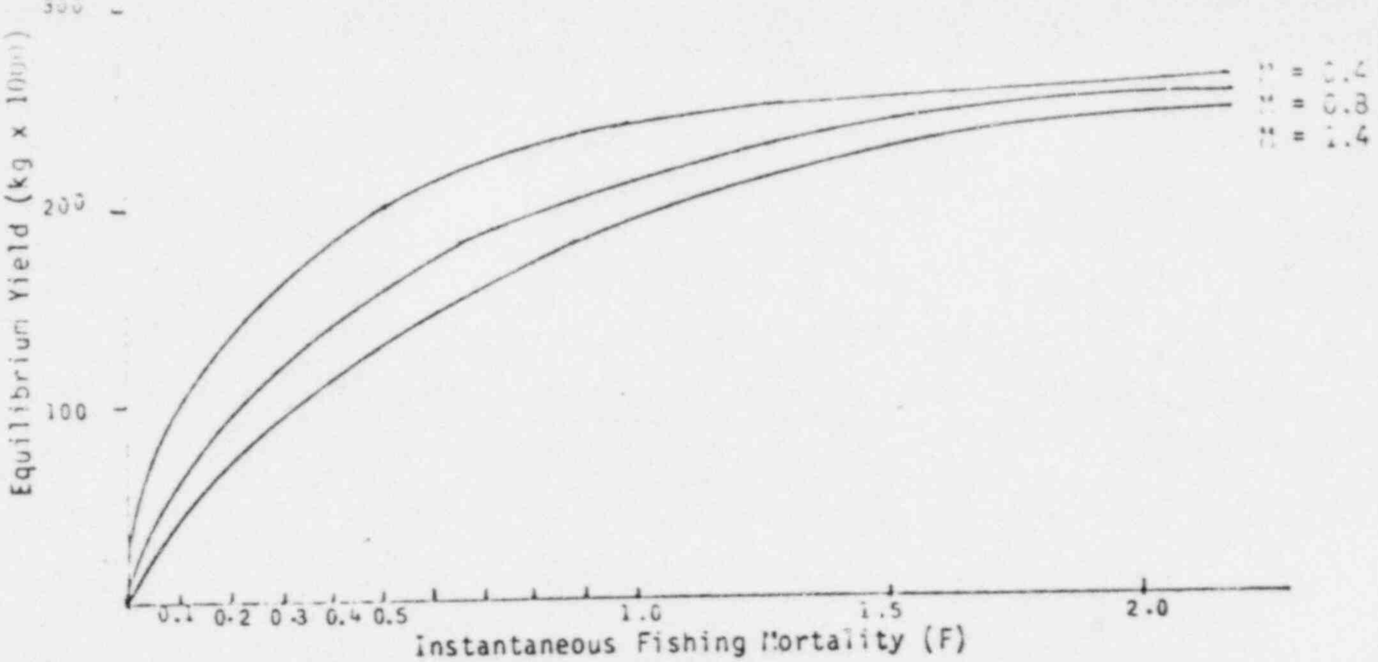

Figure 13. Equilibrium yield (kg) at various combinations of fishing (F) and natural mortalities (M increases in magnitude by 25% for age VII and onward).

numbers of older and heavier females (age VII and VIII) owing to high natural mortality; and 4) overall reduction in the size of the female population from 210,400 to 171,000 individuals (Column 4).

Of course, these predictions are valid only if spawning in the Holyoke pool from 1975 and onward does not increase progeny production beyond historical levels (1940 - 1971). Though the above condition is possible, it is more likely that substantial spawning from above the Holyoke Dam will result in greater recruitment in future generations, and that the predicted loss in yield of 23 percent should be mitigated accordingly. In the following section, an analysis is conducted to determine the relationship between equilibrium yield and hypothetical increases in progeny production due to spawning in the Holyoke pool.

b) Case 2 - increase in natural mortality with age

Following the same procedures as used in Case 1, we now examine the second possibility, namely, that natural mortality (M) increases by 25 percent for each age group following age VI. Tables 35 - 37 show the estimates of the eight key parameters at different combinations of fishing (F from 0.09 to 2.66) and natural mortality (M = 0.4, 0.8, and 1.4). However, unlike Case 1, the M values applied here are actually greater than those as stated above since the fish from age VII and older are reduced from natural causes more quickly. As a result, the proportions of repeat spawners (Column 7), catch in numbers (Column 5), average weights of individual fish (Column 9), and equilibrium yields (Column 8) are somewhat smaller than those from Case 1 (Tables 32 - 34). Results from Case 2 also demonstrate that as natural mortality increases, equilibrium yields (Column 8) and yield per effort (Column 10) should decline regardless of fishing rate (F). Though the yields are slightly smaller than those from Case 1, the optimum yields (Column 12) occur at the same fishing rates.

Figure 13 reveals the relationship between equilibrium yield (kg) and fishing mortality (F) at each of three levels of M. The curves are almost identical to those from Case 1 (Figure 12), and we note again that no maximum yield is discernable from the curves.

At the present rate of fishing (F = 0.27), results from Case 2 show that equilibrium yields from both fisheries should decline from 109,100 kg to 84,400 kg (Column 8, Tables 36 and 37) with an increase in natural mortality from 0.8 to 1.4 (a 23 percent reduction). The model also indicates (Tables 36 and 37) that the following parameters of the population should decline: 1) repeat spawners from 33.2 to 18.5 percent; 2) average weight per fish from 2.148 kg to 2.054 kg; and 3) the size of the female population from 208,100 to 170,600 individuals.

After examining the relationship between equlibrium yield and fishing mortality (Figures 12 and 13), it is apparently immaterial which of the two assumptions concerning natural mortality (Case 1 of 2) is employed. Both analyses lead to the same conclusion that an increase in natural mortality (M) will result in substantial losses in yield unless progeny production emanating from the Holyoke pool enhances virgin recruitment beyond the historical levels (1940 - 1971).

Because the results of this analysis are consistent with our present knowledge regarding the theory of fishing, the application of the Thompson-Bell model to estimate equilibrium yield appears justified. As mentioned earlier, the yields and all other parameters computed are valid only at low and intermediate rates of fishing (F 0.09 to 0.69) since yields at higher fishing levels could not be sustained in future generations due to reductions in both the parent stock and recruitment. Moreover, I should reemphasize that the conclusions from this model apply to steady state conditions which assume among other things that virgin recruitment, growth, and natural mortality remain constant, or if variable only moderately so and without trend. Though the level of virgin recruitment was essentially constant from 1966 - 1974, this condition has clearly not prevailed during the period 1940 - 1977. Indeed variations in virgin recruitment have occurred, and the factors which influence progeny survival should be examined before management strategies are contemplated.

STOCK-RECRUITMENT AND DENSITY-DEPENDENCE

In the previous section, the use of the Thompson-Bell model for computing equilibrium yield assumes that virgin recruitment is constant and maintained by relatively low egg production. Though fish populations in general, and Connecticut River shad in particular, exhibit variations in year class abundance, it is generally true that fish populations maintain themselves within relatively narrow limits. This is remarkable, especially after considering that many teleost fishes have the potential for producing tremendous numbers of progeny due to their high fecundity, which is quite unprecedented among other vertebrates. Thus stable recruitment even at low parent stock can occur only if survival of larvae and juveniles is inversely related to the size of the parent stock. Accordingly, some type of compensatory mechanism must become operative when stock abundance is below or above some critical level. This mechanism has been referred to as density-dependent mortality (Nicholson, 1954). In any natural population, the processes governing growth and mortality must act in a compensatory manner if the population is to remain within reasonable limits; that is, neither proceeding toward extinction nor completely overrunning its habitat. For marine and anadromous fishes, certain investigators (Gulland, 1965; Hempel, 1965; Dragesund and Nakken, 1971; Cushing, 1974; Daan, 1975) have reported that compensatory limits on abundance and growth occur during the larval and juvenile stages. Once a fish has matured to the adolescent and adult stages, it is commonly believed that natural mortality no longer varies with density (Beverton, 1962; Cushing, 1977). For this reason, the problem of density-dependence is concerned only with the size of the spawning stock and the resultant progeny, a fixed proportion of which become adults in the filial generation under average environmental conditions.

An important aspect in management of Connecticut River shad is the close regulation of fishing effort to ensure that enough adult shad reach the spawning

Table 38. Estimates of the total run of females, adjusted commercial catches, adjusted sport catches, female parent stock (P), and female recruitment (R), 1940 through 1971.

	(1)	(2)	(3)	(4)	(5)
Year	Initial population of females	Adjusted commercial catch (female)	Adjusted sport catch (female)	(P) Female[1/] escapement	(R) Estimated female recruitment
1940	273,000	55,901	5,149	211,950	193,312
1941	365,500	73,107	7,980	284,413	188,187
1942	308,000	64,556	6,277	237,167	156,009
1943	331,000	94,225	7,585	229,190	134,504
1944	336,000	125,050	11,321	199,629	112,747
1945	261,000	129,869	7,856	123,275	88,306
1946	282,000	176,142	5,102	100,756	102,889
1947	210,000	128,713	6,148	75,139	128,503
1948	193,000	102,366	4,337	86,297	113,688
1949	157,500	77,316	5,312	74,872	96,589
1950	115,500	46,986	3,946	64,568	79,660
1951	156,000	60,714	5,943	89,343	84,528
1952	199,000	74,092	4,860	120,048	128,228
1953	155,500	75,522	6,207	73,771	163,347
1954	137,500	56,130	4,271	77,099	165,716
1955	107,500	42,430	6,278	58,792	168,668
1956	120,500	40,684	6,342	73,474	169,092
1957	202,500	53,930	10,698	137,872	157,053
1958	246,000	82,080	12,457	151,463	122,957
1959	237,500	73,381	14,762	149,357	119,251
1960	246,500	84,379	7,905	154,216	133,141
1961	246,000	91,609	5,074	149,317	129,387
1962	227,000	82,275	9,877	134,848	125,072
1963	162,000	60,987	16,585	84,428	104,953
1964	174,000	53,604	19,401	100,995	112,424
1965	200,000	60,391	9,942	129,667	[illegible],782
1966	183,500	51,467	11,346	120,687	143,752
1967	184,000	42,532	8,763	132,705	108,623
1968	140,000	33,025	7,138	99,837	110,780

continued

Table 38 continued

	(1)	(2)	(3)	(4)	(5)
Year	Initial population of females	Adjusted commercial catch (female)	Adjusted sport catch (female)	Female[1/] escapement	Estimated female recruitment
1969	166,500	45,333	6,409	114,758	127,920
1970	209,500	43,534	5,967	159,999	168,162
1971	214,000	45,578	8,315	160,107	227,310

1/ Female escapement = initial population of females - (commercial and sport catches).

grounds. This objective can be attained only after we obtain a more thorough understanding of the shad's stock-recruitment relationship. In practice, the relationship between escapement of adults and subsequent recruitment in the next generation is not constant, but may be highly variable. This variation is due to a combination of biotic (predation, interspecific and intraspecific competition for food, territoriality) and abiotic (water temperature, discharge rates) factors. At present, owing to our superficial knowledge regarding the growth and mortality of post-larval and juvenile shad, it is impossible to arrive at a conclusion as to which of the above factors are most influencial.

One form of the stock-recruitment relationship has been developed by Ricker (1954):

$$R = Pe^{a(1-{}^{P}/{Pr})} \qquad (27)$$

where R = numbers of recruits

P = numbers of spawners

a = constant from the regression of P on $\log_e ({}^{R}/{P})$

Pr = constant from the regression of P on $\log_e ({}^{R}/P)$,

and another by Beverton and Holt (1957):

$$R = {}^{1}/aP+B \qquad (28)$$

where R = numbers of recruits

P = numbers of spawners

a = constant from the regression of P on P/R

B = constant from the regression of P on P/R.

However, it should be emphasized that these models are simply two members of a general family of extinction curves that have been developed to analyze reproduction in fish populations.

Both models will be fitted to the parent stock and recruitment data from 1940 through 1971 (Table 38). Virgin recruitment (Column 5) was computed previously (see page 108), whereas parent stock (Column 4) was determined by subtracting the adjusted commercial (Column 2) and sport catches (Column 3) from the initial population of females (Column 1). Leggett (1976) found that the total sport catch was on the average 2.327 greater than that from the Enfield area. Thus, the sport catches from Enfield (Connecticut Department of Environmental Protection, unpublished data) were multiplied by 2.327 so as to provide an estimate of the total sport catch. The parent-progeny relationship shown here is in equivalent units (number of mature female shad). This technique is somewhat of a compromise, and may be considered by some as not the most effective approach, since progeny production may relate more to adult biomass and fecundity than to adult numbers. Yet, these alternative techniques also have their limitations, because stock biomass and average fecundity will themselves change with corresponding alterations in the age composition and spawning history, particularly in response to fishing and natural mortality. Thus, I contend that stock numbers will provide an adequate representation of stock-recruitment.

A curve of the Ricker model (equation 27) was obtained by fitting a linear regression to $\log_{10}$ (R/P) against P (Column 4 Table 38). Further details of this computation are presented in Appendix 2. The empirical curve of stock-recruitment using the Ricker model is illustrated (dotted line) in Figure 14. The mathematical expression for computing recruitment is

$$R = Pe^{0.8586(1-P/162)}.$$

The correlation coefficient ($r = 0.754$) for the Ricker model was significant ($t = 6.29$, d.f. = 30, $p<0.001$), indicating that the observed data was well approximated by the empirical expression.

A reproductive curve of the Beverton-Holt type (equation 28) was obtained by regressing P/R against P (see Appendix 3). The empirical curve is presented (solid

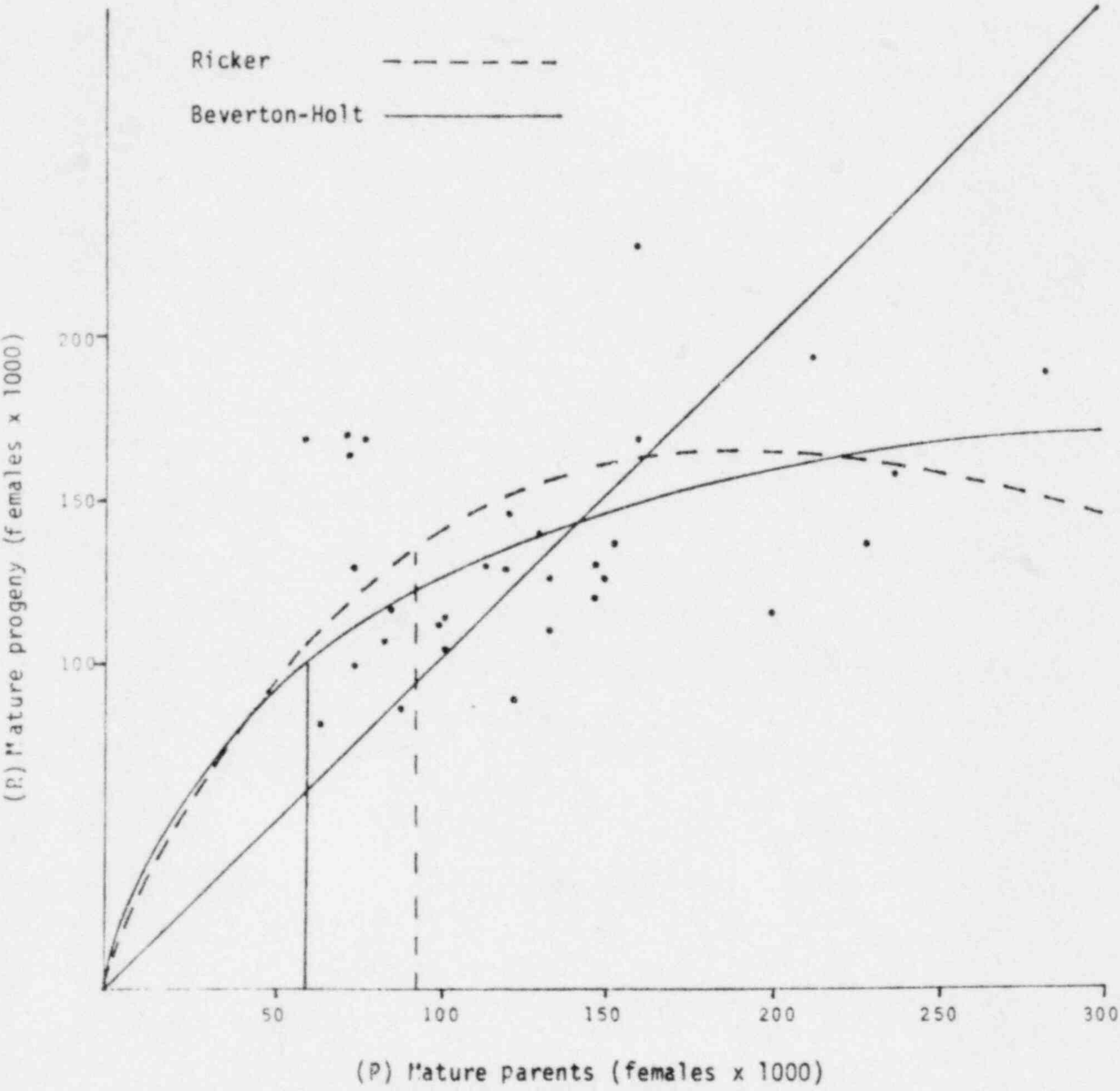

Figure 14. Emperical curves of stock-recruitment using both the Ricker (-----) and Beverton-Holt (———) models, 1940 - 1971.

line) in Figure 14, and the model when fully developed is

$$R = {}^{1}/(0.00488 + 0.2981/P).$$

The correlation coefficient ($r = 0.803$) of the regression was also significant ($t = 7.38$, d.f. = 30, $p<0.001$).

Because the parent-progeny relationship developed from either model is depicted in equivalent units (numbers of mature females), it is justified to draw a 45° transfer line in Figure 14 to determine surplus production. Recruitment above this line is in excess of that required to replace the parent stock, and this surplus represents the number of female shad which can be harvested if the shad run is maintained at an equilibrium. For a single-age stock like that of the Pacific salmon, where the 45° transfer line intersects the curve, the stock will just replace itself in the absence of fishing. However, in a multi-age stock like that of the American shad, annual variations in adult natural mortality (M) will produce deviations in the replacement level. Moreover, the presence of repeat spawners will influence not only the position of the replacement stock, but also the amplitude of the reproductive curves and the amount of surplus production that could be harvested annually. For example, if repeat spawners comprise on the average 30 percent of the run, the total run in the filial generation will be 30 percent greater than that predicted by the model. As a result, maximum sustainable yield cannot be computed directly from the reproductive curves in Figure 14 without additional information regarding repeat spawning rates and natural mortality rates.

It should be pointed out, however, that the general shape of the reproductive curve is unaffected by the presence of repeat spawners, because the curve is thought to be species specific and related to the fecundity of the stock (Cushing, 1971). Using the parameters of the Ricker model, Cushing and Harris (1973) compared the stock-recruitment relationship for the cod, Gadus morhua; and for certain species of salmon, herring, and flatfish. They concluded that related species have very similar reproductive curves, and that the dome of the curve becomes higher as average fecundity increases. For example, the cod, being a highly fecund fish with an ova capacity in the order of 7 - 10 million eggs per female, was shown to have the highest dome, whereas, the salmon species, with an average female fecundity of between 3 and 6 thousand ova, were found to have the lowest. In addition, they examined the reproductive curves for the Atlantic herring, Clupea harengus, and Pacific herring, C. pallasi and reported that both species had moderately low-domed reproductive curves with (a) values ranging from 0.45 to 1.06. The (a) value (0.8586) computed here for the American shad, is well within the range of values determined for other clupeids thereby substantiating the findings by Cushing and Harris (1973) that reproductive curves are similar among related species.

In spite of the fact that the empirical curves for the shad cannot provide direct estimates of optimal escapement and maximum sustainable yield, a close examination of these curves is justified because they do show some interesting contrasts and similarities. According to the Beverton-Holt curve (Figure 14), progeny production in the succeeding generation begins to level off as the numbers of female spawners exceed about 125,000. In addition, when parent stock is less than the theoretical replacement level (145,000 spawners), recruitment never exceeds the replacement level. Assuming no repeat spawners, maximum surplus production of recruits occurs at the greatest vertical distance between the 45° line and the empirical curve (as indicated by the solid vertical line in Figure 14). Thus a female stock of about 60,000 individuals will produce about 100,000 virgin females in the filial generation resulting in a surplus yield of some 40,000 virgin females annually. However, if female escapement drops to below 50,000 individuals, recruitment in the next generation would decline rapidly as evidenced by the steep ascending limb of the curve. The dome-shaped curve for the Ricker model (Figure 14) shows that recruitment reaches a maximum at about 160,000 spawners then declines thereafter with increases in spawner abundance. Assuming no repeat spawners, maximum surplus of recruits is attained by a female spawning stock of about 80,000 individuals (as indicated by the dotted vertical line in Figure 14) which produces about 125,000 virgin females in the filial generation resulting in a surplus yield of about 45,000 virgin females annually. However, if the female spawning stock declines to a level below 70,000 females, virgin recruitment in the next generation would diminish rapidly.

As mentioned previously, variations in year class strength supporting the American shad fishery have occurred in the Connecticut River. Year classes 1940 and 1941 appeared to be stronger than those for subsequent years (Column 5, Table 38). In fact, year class recruitment became progressively weaker from 1942 - 1952 followed by a resurgence in recruitment from 1953 - 1957. Except for year classes 1970 and 1971, cohorts from 1958 and onward can be characterized as of moderate strength. This illustrates the great importance attached to virgin recruitment as a variable in the formation of the shad stock, and in developing a biological foundation for fishery regulations.

Due to the fact that virgin females comprise between 70 and 80 percent of the female run annually, variations in the magnitude of the run is clearly traced to deviations in virgin recruitment which is thought to be influenced by one or a combination of two factors. One is density-dependent mortality (competition for food, predation, territoriality) which increase in dimensions as the numbers of ova, larvae and juveniles increase. The other is density-independent mortality (random climatic and environmental factors - water temperature, discharge rates, precipitation, etc.) which is thought to reduce the progeny numbers regardless of density. The results of the stock-recruitment analysis for the Connecticut River

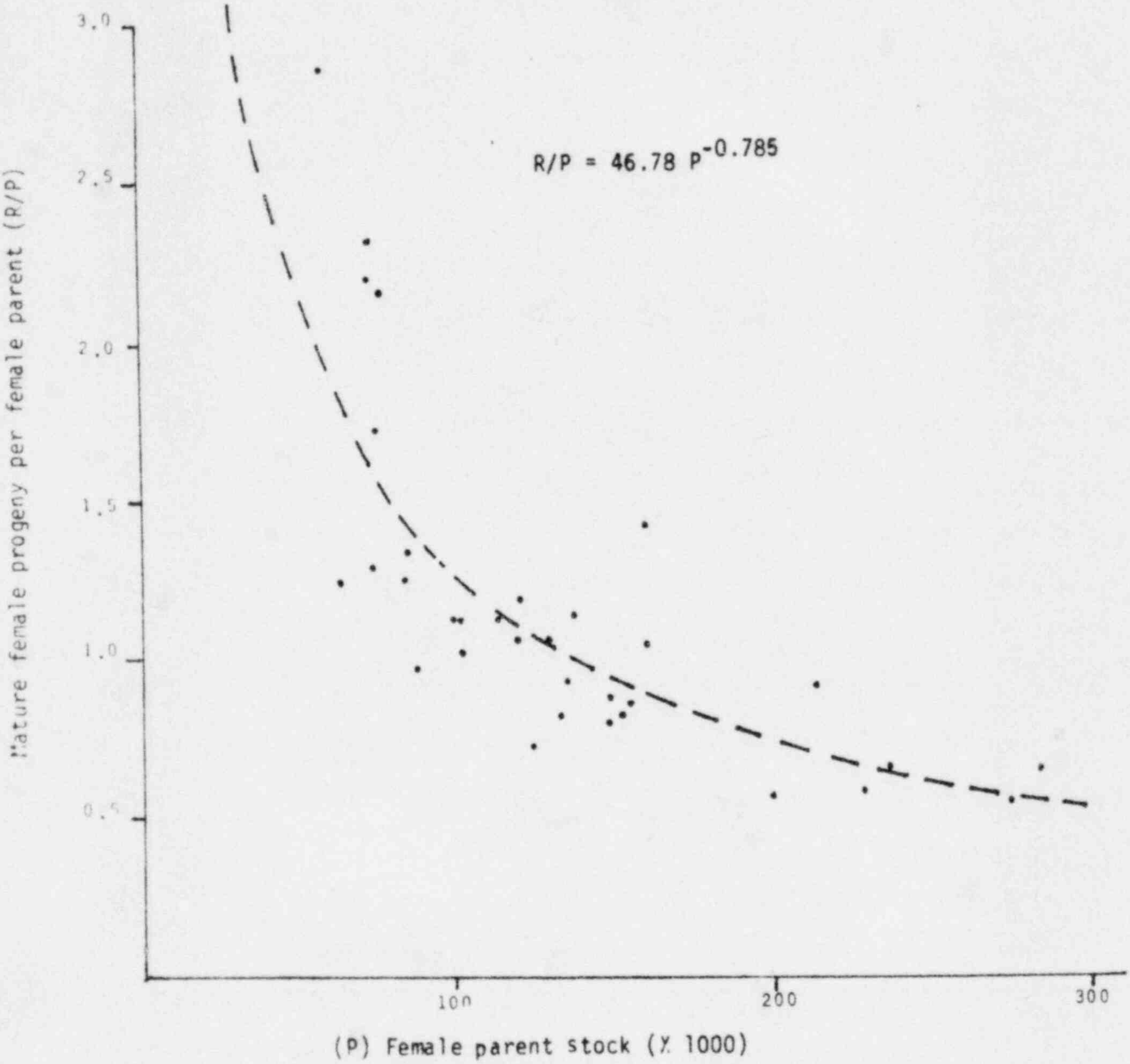

Figure 15. Relationship between the ratio of mature female progeny per female parent (R/P) and the size of the female parent stock (P), 1940-1971.

shad (Figure 14) suggest that the formation of year class abundance is greatly influenced by density-dependent factors. This hypothesis is further strengthened by Figure 15, which illustrates the relationship between the ratio of mature female progeny/female parent and the size of the female parent stock. These data were fitted to a power curve of the type:

$$R/P = aP^b$$

where R/P = ratio of mature virgin females per female parent

P = numbers of female parents

a = y- axis intercept

b = slope of the regression.

The inverse correlation coefficient (-0.805) was significant ($t = 7.43$, d. f. = 30 $p = <0.001$) suggesting that survival of mature progeny per parent declines in a curvilinear fashion as the parent stock increases. Furthermore, this relationship implies that year class abundance is not directly influenced by random variations in climatic factors, but by factors which become more effective as the progeny increase in abundance. This is not meant to suggest that climatic and environmental variables are unimportant, but rather that their influence upon year class strength may be manifested in exceedingly complex ways. These effects will be discussed further below.

Studies into the early life stages of various marine fishes (principally, Sette, 1943; Ahlstrom, 1954, 1966; Pearcy,1962) suggest that density-dependent regulation is more likely to occur during the larval and early juvenile stages, rather than during the late juvenile, adolescent, or adult phases. This is because the larvae and early juveniles grow exponentially, require an immediate food source following yolk sac absorption, are essentially planktonic, and posses a limited searching capability. Hence during these stages, density-dependent processes (predation and competition for food) are believed to be most operative. For the Atlantic herring, *Clupea harengus*, Cushing and Bridger (1966) reported a significant

Table 39. Juvenile catch/effort for year classes 1966 - 1972 and the numbers of age V virgin females occurring in the run five years later.

Year class (x)	Juvenile catch/effort[1/]	Age V females[2/] (x+5)
1966	8.7	103,704
1967	9.1	66,663
1968	3.6	80,444
1969	7.9	90,136
1970	11.6	122,119
1971	30.9	179,302
1972	2.6	78,263

1/After Marcy (1976, Table 97, page 159)

2/ Taken from Column 4, Table 28.

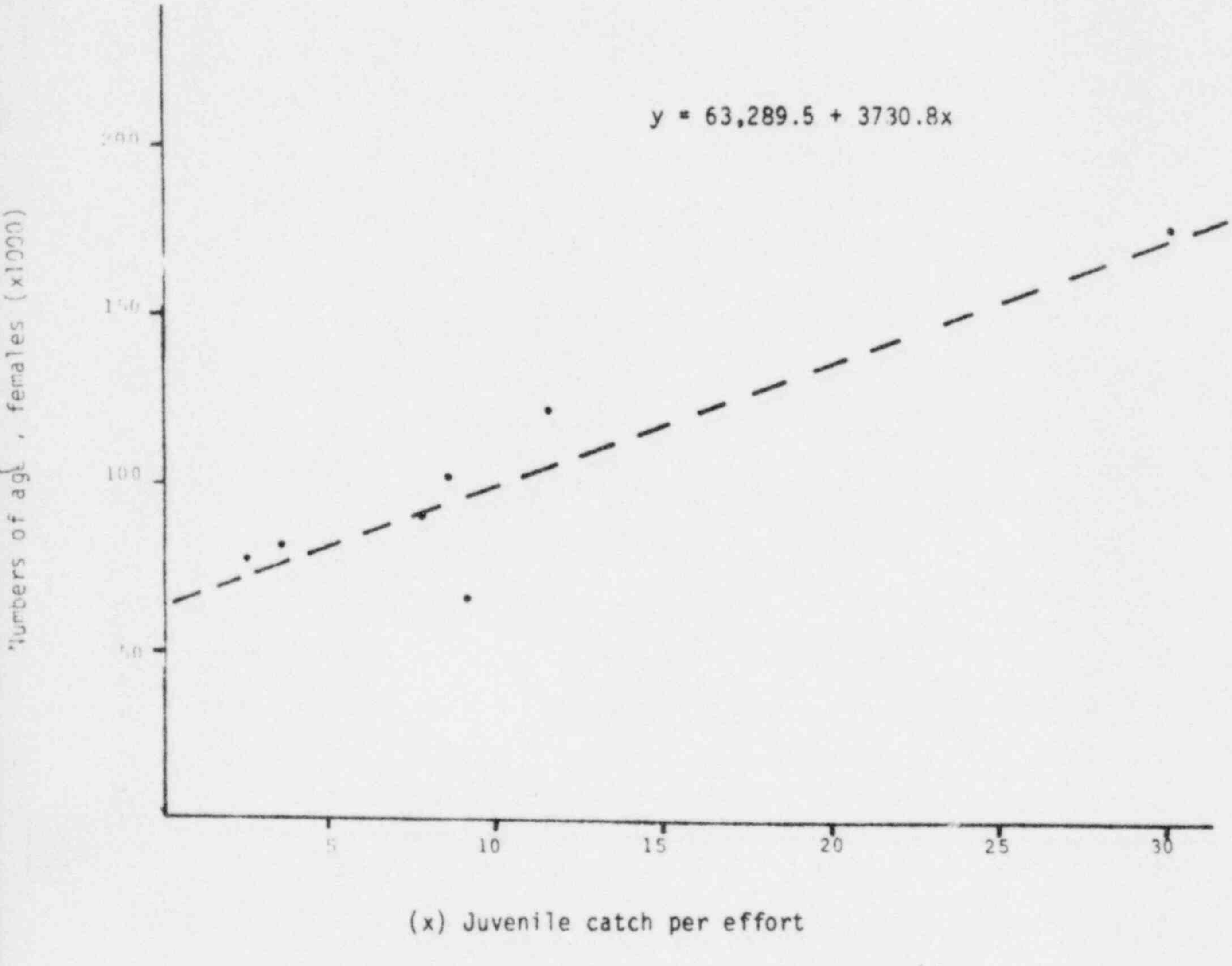

Figure 16. Relationship between the catch/effort index[1] of juvenile shad, 1966-1972, and the numbers of age V females[2] of the same year class, 1971-1977.

[1] After Marcy (1976, Table 97, p. 159)

[2] Data taken from column 4, Table 28.

linear dependence of larval abundance on parent stock, and an asymptotic one of subsequent recruitment upon larval abundance. In this study, similar evidence exists for Connecticut River shad. Catch/effort data of juvenile shad from below Holyoke for the 1966 - 1972 year classes (after Marcy, 1976, Table 97, page 159) and the estimated numbers of Age V females occurring five years later are shown in Table 39. These data were fitted by linear regression (Figure 16) and the results revealed a positive correlation ($r = 0.924$) which was highly significant ($t = 5.40$, d. f. = 5, $p < 0.01$). This finding clearly suggests that variations in juvenile abundance is closely associated with fluctuations in the numbers of virgin females of the same year class; thus, year class formation appears to occur during or before the juvenile stage.

The density-dependence thesis for Connecticut River shad is further supported by the ratio between the strongest (1971) and weakest (1950) year class (column 5, Table 38). Year classes 1971 and 1950 are estimated in terms of female virgins as 227,310 and 79,660, respectively, resulting in a ratio in the order of 2.8:1. This ratio is relatively small and suggests that the mechanism controlling year class strength is surprisingly stable. The importance of this has to be considered in relation to the total mortality rate (Z) occurring from egg to virgin recruitment Depending on ovarian weight, an Age V female shad will produce annually from 200,000 to 280,000 ova (Leggett, 1969). Assuming no repeat spawners, for the shad run to replace itself in the filial generation, each female would need to generate two adults (one male and one female) out of say 220,000 ova. Owing to the relatively high fecundity of a female shad, the population certainly possesses the potential of producing millions of recruits in the next generation. Consequently, the instantaneous rate of total mortality (Z) from egg to virgin recruitment must not only be high, but very stable to account for the minor variations in year class

Table 40. Example showing the changes in female virgin recruitment with a 10 and 20 percent alteration in total mortality (Z) from ova to virgin recruitment.

During 1970, some 160,000 females (Column 4, Table 38) produced approximately 168,200 virgin females (Column 5, Table 38). Assuming an average female fecundity of 220,000 ova, total egg production in 1970 was 3.52×10^{10} ova (i.e. 220,000 ova x 160,000 females). Survival (S) from ova to virgin recruitment was:

$$0.000048 = {}^{168200}/_{3.52 \times 10^{10}\ \text{ova}}.$$

The instantaneous total mortality (Z) from ova to recruitment is:

$$12.25 = -\ln(0.0000048).$$

Change in Z	Z	Survival (S)[1/]	Numbers of virgin females[2/]
+10%	13.48	0.0000014	49,280
-10%	11.03	0.0000162	570,240
+20%	14.70	0.0000004	14,080
-20%	9.80	0.0000555	1,953,600

[1/] $S = e^{-Z}$

[2/] Numbers of virgin females = $S(3.52 \times 10^{10}$ ova) abundance. This is best illustrated by an example. According to Column 4 of Table 40, some 160,000 adult females in 1970 had produced approximately 168,200 virgin females in the next generation. Assuming that the average fecundity of a female is 220,000 ova, total ova production during 1970 was 3.52×10^{10} (i.e. 220,000 x 160,000). Accordingly, female survival from ova to recruitment is:

$$0.0000048 = {}^{168200}/_{3.52 \times 10^{10}}$$

or approximately one virgin female per 220,000 ova. In this example, the instantaneous rate of total mortality (Z) was computed as

$$12.25 = \ln 0.0000048.$$

If Z (12.25) was to vary annually by ± 10 percent (11.03 to 13.48), the ratio of virgin female production would be about 11.6:1; that is 570,240 virgin females are produced with a 10 percent reduction in Z, and 49,280 when Z is increased by 10 percent (Table 40). Moreover, fluctuation in Z of ± 20 percent results in an astronomical ratio of 138.8:1. It follows that deviations in natural mortality (Z) in the order of 10 to 20 percent would generate dynamic fluctuations in year class strength, the magnitude of which is certainly not manifested in the observed data (Column 5, Table 38). Due to the relatively high fecundity of Connecticut River shad, the population produces ova greatly in excess of the ultimate recruitment to the adult stock. This suggests the occurrence of very high egg and larval mortality rates. Thus the factors affecting mortality from hatching to virgin recruitment whatever they may be must occur regularly and with monotonous precision. If the regulation of year class abundance was due primarily to climatic factors, the adult shad population would then be expected to exhibit erratic oscillations in abundance, since these factors are believed to reduce the population regardless of density. Even if we assume for a moment that climatic factors do directly influence recruitment, it is difficult to comprehend the manner in which these factors confer stability to a fish population. It is more difficult to understand how a declining population could ever recover to its former levels, if year class strength is controlled by random processes.

Though the available evidence is circumstantial, the formation of year class abundance in Connecticut River shad appears to occur during or before the juvenile stage. Natural mortality between hatching and virgin recruitment was shown to be high, yet the variance of recruitment to the shad stock was relatively low. This certainly implies that a compensatory mechanism must exist to stabilize recruitment at the observed levels.

Because shad are broadcast spawners, neither territoriality nor the competition for nesting sites can be considered as valid factors in the regulation of recruitment. In addition, predation by piscivorous fishes and invertebrates, as well as intraspecific competition for food are known to regulate numbers in a density-dependent manner.

For predation to be solely responsible in controlling year class strength, one must imagine a chain of predators each appearing in sufficient numbers and at the right moment to reduce the ova, larvae and juveniles at the rate of about 5 to 10 percent per day. This could occur only if the abundance of predators was instantaneously linked to the number of prey. Such a mechanism however, is unrealistic since there is usually a time lag between increases in predator abundance to that of their prey.

The second factor, intraspecific competition for food, in combination with predation appears to provide a more workable hypothesis. In the first place, large numbers of female spawners are expected to produce dense concentrations of larvae. Following yolk sac absorption, these larvae will require an immediate source of zooplankton. Thus, the degree of intraspecific competition may be a function of the larval and zooplankton densities. When larval abundance is high, competition for food may be severe enough to either eliminate larvae outright, or greatly weaken them so that they become more vulnerable to predation.

Because shad larvae grow rapidly, and because they can do little but drift in the current, their mortality rates are thought to be high. If the regulation of numbers is a density-dependent process, then the only simple link between larval mortality and growth is the availability of food. Thus, intraspecific competition for food during the post-larval drift (following yolk sac absorption) may be the primary mechanism that determines year class strength in the shad population. The duration of the so-called "critical period" (Hjort, 1926) may last for a few days, or until the post-larvae have fully metamorphosed into the juvenile stage.

If the zooplankton production cycle, the source of post-larval food, deviates randomly in periodicity, amplitude and duration, the shad should spawn at some time interval near the height of the production cycle. In an evolutionary sense, the American shad may have developed into a spring spawner to take advantage of the spring production cycle. In a given year, highest survival of larvae and the strongest year-classes may be produced by the best match of shad larvae and that of their food. Conversely a mismatch between the production cycles would generate greater competition for food and poorer survival of larvae. Therefore, according to the hypothesis presented herein, variations in year class strength are primarily a function of intraspecific competition for food during the post-larval drift, the magnitude of which is modulated by a match or mismatch of the larval production cycle to that of their food.

In most temperate lakes and rivers, spring maxima generally occur among crustacean zooplankton and in particular among cladocerans (Birge, 1898; Brooks, 1946; Greenburg, 1964; Hall, 1964; Cummins et al., 1969; Cramer and Marzolf, 1970). According to Hall (1964), abrupt increases in cladoceran abundance during late spring are believed to reflect a food-limited system in which phytoplankton become abundant due to increases in the concentration of nitrogen and phosphorous in the upper layers of water. Herbivorous cladocerans (i.e. Bosmina sp. and Daphnia sp.) then respond by grazing extensively on the phytoplankton community. Increases in the cladoceran feeding rate apparently induce reproduction, and the density of these plankters markedly increase soon thereafter. The cladocerans eventually graze down the phytoplankton, and a decline in cladoceran abundance ensues as a result of a food shortage. Thus, the relationshop between cladoceran and algal abundance is essentially a predator-prey mechanism. The timing, amplitude and duration of the cladoceran production cycle being directly affected by the biotic and abiotic variables which influence algal abundance.

In the Connecticut River, Massengill (1976) reported that the cladoceran, Daphnia spp., was the most dominant zooplankter encountered in the vicinity of the Connecticut Yankee Nuclear Power Plant, Haddam, Connecticut. Although this study was conducted some 40 km. below the major spawning areas, the results may be applicable. During the two year period 1971 - 1972, a distinct peak in cladoceran abundance occurred on June 24, 1971 and on June 27, 1972, but the amplitude in June 1971 ($40,914/m^3$) was almost ten times greater than that ($4,445/m^3$) in 1972 (Massengill, 1976, Table 13, page 57). After considering that in terms of female recruits, the 1971 year class was clearly much stronger than the 1972 cohort, these findings suggest that variations in the amplitude of the cladoceran production cycle during June are linked to the formation of year class strength. This hypothesis is further supported by the food habit study conducted on juvenile shad by Marcy (1976). He reported that compared to all other taxa found in the stomachs of juveniles collected prior to September 8, 1968, cladocerans comprised the greatest volume. Unfortunately stomachs from juveniles smaller than 39 mm (total length) were not examined.

For the limiting food hypothesis to be realistic, a number of postulates regarding growth and mortality of larvae are assumed true. Firstly, it is assumed that larval growth rates are genetically predetermined and thus are unalterable. Mortality will then occur whenever the post-larvae fail to obtain enough food to sustain this innate growth rate. This postulate is an essential element to this hypothesis, since during the post-larval stage, intraspecific competition for zooplankton must somehow result in substantial mortality either from starvation or predation. Although I have been unable to locate any published accounts conclusively demonstrating that larval growth is genetically predetermined, or that post-larvae actually starve in the natural environment, observations by various researchers are at least consistent with this postulate. For instance, Blaxter (1971) determined the condition factor (Fulton's coefficient) for Atlantic herring larvae, *Clupea harengus*, taken from the wild, and compared them to herring larvae held in aquaria for a few days at various zooplankton densities. He found that the condition factors for most wild larvae greater than 12 mm. (post-larvae) were most similar to those kept in a starvation state. This implies that many larvae in the natural system may actually starve to death. Further support comes from a study by Riley (1966) who kept larval plaice, *Pleuronectes platessa*, in aquaria with low zooplankton densities. After a few days, he reported that many larvae became progressively more deformed as they approached metamorphosis suggesting that post-larvae maintained at low food abundance may be sufficiently weakened as to become more vulnerable to predation. O'Connell and Raymont (1970) examined the mortality of anchovy (*Engraulis mordax*) larvae during the first 12 days of life at various food densities and found containers of larvae receiving 1000 copepod nauplii/l/day or less showed drastic mortality on the 6th and 7th days after hatching, while containers receiving 4000 nauplii/l/day or more showed no such trend. Thus, O'Connell and Raymont concluded that food concentration could influence larval survival and ultimately year class strength of the anchovy.

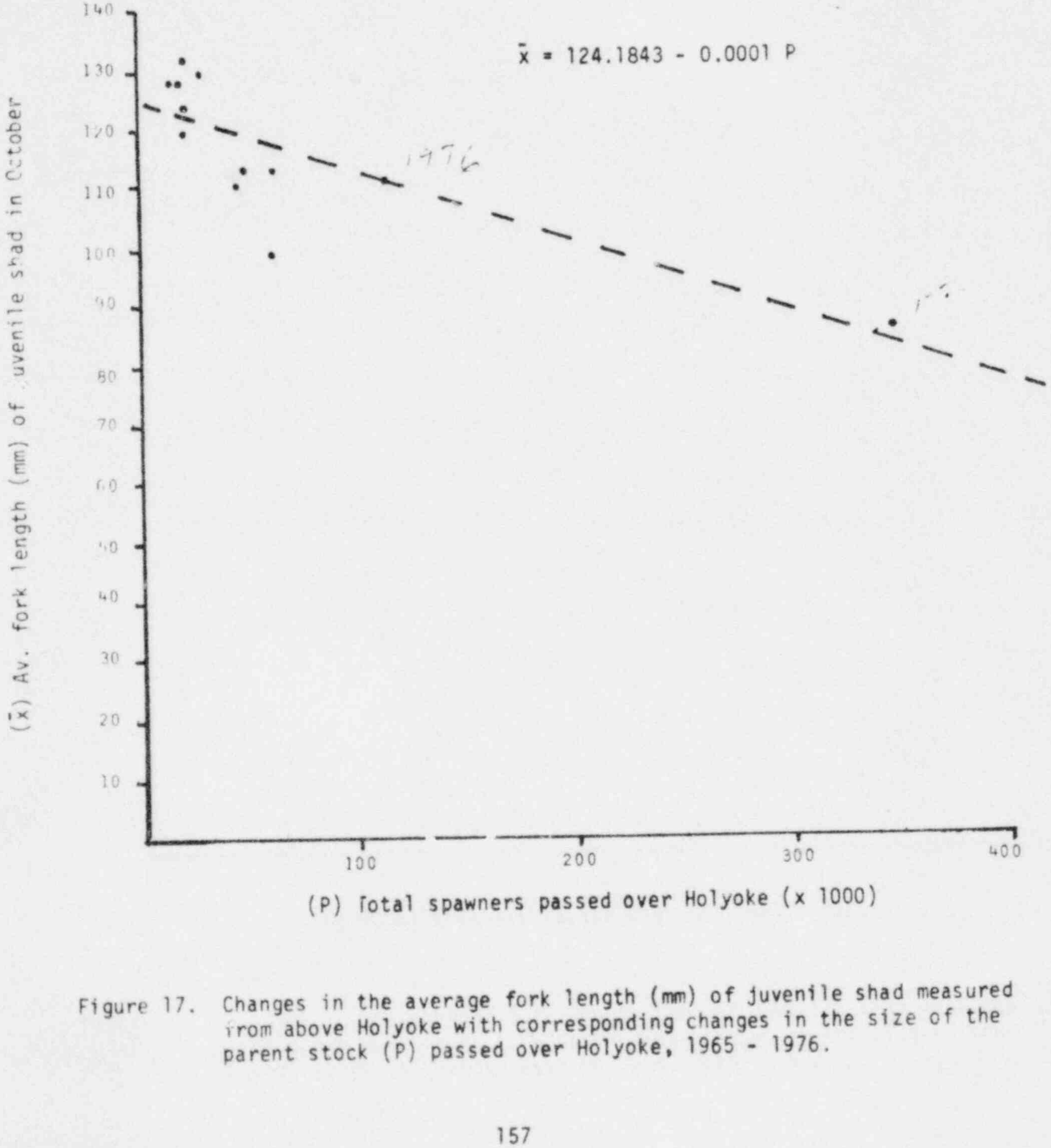

Figure 17. Changes in the average fork length (mm) of juvenile shad measured from above Holyoke with corresponding changes in the size of the parent stock (P) passed over Holyoke, 1965 - 1976.

Furthermore, Lasker et al. (1970) examined the effect of delayed feeding on the survival of newly hatched anchovy (E. mordax) larvae. They found that feeding could be delayed up to 1.5 days after yolk sac absorption without enhancing mortality. Yet a delay of 2.5 days resulted in catastrophic mortality even if food were made available.

As opposed to larval growth, juvenile growth is believed to be density-dependent and whenever a juvenile shad fails to procure sufficient food it simply grows more slowly. This is reasonable because juveniles are mobile, possess a much greater searching capability, and thus possess more omnivorous food habits than the larvae. Hence, mortality resulting from starvation is not expected to occur during the juvenile stage. Unlike the previous postulate regarding larval and post-larval growth, compensatory growth of juvenile shad is much less speculative. For example, given in Figure 17 is the relationship between the average fork lengths (mm) of juvenile shad collected during October form above the Holyoke dam, and the size of the parent stock annually transported over Holyoke from 1965 - 1976 (Dr. Roger Reed, personal communication). Linear regression analysis was performed to determine whether an association existed between juvenile length and the abundance of adult shad. Results revealed a significant inverse correlation ($r = -0.797$, $t = 4.17$, d.f. = 10, $p < 0.01$); that is, as the parent stock annually passed at Holyoke increased in abundance, the average fork length of juveniles measured in October diminished in size. This illustrates that juvenile growth rates are inversely proportional to their density suggesting some type of growth compensation.

Secondly, zooplankton organisms are distributed in patches (Hutchinson, 1961; Cassie, 1963) so that some larvae encounter a multitude of food while others obtain much less, and die either from starvation or from predation. Thirdly, an individual larvae will spend only a short length of time within a given patch of zooplankton.

This is because both the larvae and zooplankton will be continuously changing their position in space and time, so that few post-larvae and early juveniles obtain enough food for survival to full juvenile status. Lastly, climatic factors are expected to influence year class strength by directly affecting the periodicity and amplitude of the spring pulse of algae and zooplankton. Thus an apparent positive correlation between mean June water temperature and year class strength would be construed here not as a cause and effect relationship, but rather as evidence of an indirect casual connection; the real dependent variable being the algal and/or zooplankton production cycles. In other words, year class strength is indirectly dependent on conditions in the external environment during the transition to active feeding by the post-larval shad. Thus, fluctuations in the biomass of the zooplankton community are considered here as being directly related to algal production, the water temperature regime, the force and direction of current, and to other yet unknown processes affecting the interaction between air and water.

In addition to intraspecific competition for food during the post-larval drift, predation of juvenile shad may also be important in determining year class strength. For example, let us suppose that most shad larvae exhaust their yolk sac near the peak of the zooplankton production cycle. Under these conditions, more larvae would survive to full juvenile status. But because juvenile abundance is high, intraspecific competition for food should be magnified, thus resulting in a compensatory decline in growth rate. As a consequence, these slower-growing juveniles would be subjected to a greater rate of predation, since they are exposed longer to a predator's range of interest. Conversely, if larvae reabsorb their yolk sac near the end of the production cycle, intraspecific competition for food would be greater, and fewer larvae would survive to the juvenile stage. These surviving juveniles would be exposed to less intraspecific competition for food, and thus would grow more rapidly and suffer less predation.

Predation of juveniles is viewed here as a subsidiary mechanism in the stabilization of year class abundance. This is because the intensity of predation upon juvenile shad will vary not only as a function of prey growth and abundance, but as a function of predator abundance as well. During certain years, when predator abundance is low, density-dependent predation on juveniles may be a minor source of regulation.

In summary, the density-dependent mechanism proposed here is a two-fold process: first, the progeny are drastically reduced during the post-larval drift by intraspecific competition for zooplankton. The growth rate of larvae is rapid and assumed to be genetically pre-determined. Thus post-larval shad suffer mortality whenever they fail to acquire enough food to sustain their innate growth rate. Secondly, compensatory growth during the juvenile stage arises from competition for food, but density-dependent mortality is mainly the result of predation. Density-dependent mortality in the form of predation should decline with age, because as the juveniles grow to the adult stage, they become vulnerable only to the larger and less numerous predators. Furthermore, the development of dominant year classes (i.e. 1971) is probably a random chance phenomenon; this occurs whenever the larval shad exhaust their yolk sac near the peak of the zooplankton production cycle. Moreover, variation in the amplitude, periodicity and duration of the zooplankton production cycle are most likely influenced by climatic factors (i.e. water temperature, precipitation, discharge rates etc.)

This theory is biologically attractive because it provides, at the very least, a working hypothesis, as to the manner in which density-dependent mortality could occur in a broadcast spawner such as the American shad. In addition, it offers an explanation of how climatic and environmental factors can influence year class strength.

Because of the obvious importance of recruitment to the size of the annual shad run, a clearer understanding of the stock-recruitment relationship is of critical importance to successful managment of the Connecticut River shad. Due to the apparent complexity among the biotic an abiotic factors associated with the formation of year class recruitment, I contend that a great deal more research will be required before the theory of stock-recruitment becomes as useful to fishery management as the theory of equilibrium yield. Not only are the processes enormously complex, but the data base regarding post-larval food habits and juvenile growth and mortality rates are either non-existent or very fragmentary. For Connecticut River shad, these major deficiencies are partly due to the inherent problems in obtaining unbiased estimates of ova and larval abundance, and partly due to an unwillingness to alter our present research emphasis from the adult to the sub-adult stages. Problems in obtaining quantitative estimates of shad ova occur because adult shad are known to spawn after dusk so that the distribution of eggs in the water column may change dramatically between day and night samples. As for the larvae, sampling problems will occur due to net avoidance, differential clogging of the plankton nets, and to a protracted spawning season. In addition, the distribution pattern of shad larvae may also exhibit some form of diel variation.

To comprehend the density-dependent mechanism for the American shad or for any other species, it may become necessary to embark into fascinating depths of fundamental physiology, ecology, and other aspects of biology. Furthermore, the relationship between post-larval abundance and zooplankton density are considered as among the least stable, yet perhaps the most decisive process determining year class strength in the shad population, and the dynamics of this relationship ought to be extensively examined in future research. Hence more information is needed on the biology of the algal and zooplankton communities in the Connecticut River, as well as on the chemical and physical variables which influence the spring production cycle, even though such research has been traditionally outside the scope of fisheries biology.

SELF-REGENERATING MODEL

A prerequisite in developing an effective management strategy is the identification of objectives to be pursued. At present, management priorities for Connecticut River shad should be predicated on two fundamental objectives: 1) to maintain the parent stock at levels which will produce the greatest surplus of recruits; and 2) to determine the level of fishing effort which will provide an optimum yield and yield per effort for the commercial and sport fisheries. Of the two, the first is obviously overriding since any policy to reduce the parent stock and recruitment to low levels should be soundly rejected. The importance attached to the second objective probably depends more on economic, social, and political issues than on biological factors. Conflicts may arise over these objectives, the resolution of which will perhaps be the most vexing problem facing fishery biologists.

In the previous section, the definition of the shad's stock-recruitment relationship served as an integral element in developing sound management decisions. Although both stock-recruitment models (Ricker and Beverton-Holt types) can furnish rough estimates of optimum escapement and maximum surplus production, they are unable to provide information relating to maximum sustainable yield to the commercial fishery. This is because both models fail to consider the parameters of growth and natural mortality. Likewise, the Thompson-Bell yield model provided plausible estimates of equilibrium yield at various combinations of fishing (F) and natural (M) mortalities. But when the model was employed at annual rates of fishing (u_{total}) greater than 50 percent, the sustainable yields were adjudged to be unreasonably high, since a decline in the parent stock to levels below about 70,000 females would inevitably reduce recruitment and yield in future generations.

The foregoing has necessitated the development of a self-regenerating model based upon the mathematical elements of both the Ricker stock-recruitment and the Thompson-Bell yield models. The new model is essentially an equilibrium yield type with variable recruitment, and is very similar to the one developed by Beverton and Holt (1957). The self-regenerating model provides, in my judgement, a more realistic appraisal of the stock's fate during many generations and under various levels of fishing mortality, since it attempts to relate escapement and subsequent recruitment to fishing intensity. This interrelationship has long been recognized as decisive in problems of fisheries exploitation.

Following the Thompson-Bell model, the new model incorporates size specific fishing (F) mortality, constant or age specific natural (M) mortality, and age specific growth. The underlying assumptions implicit to the self-regenerating model are also the same as those for the Thompson-Bell model (see page 114) with one notable exception; that is, the magnitude of female recruitment (R) in the filial generation is no longer constant, but varies according to the size of the parent stock (P). From the previous section, the emperical relationship between stock and recruitment was computed using the Ricker equation as:

$$R = Pe^{0.8586\ (1-P/162)},$$

and for the Beverton-Holt type as:

$$R = {}^{1}/(0.00488 + 0.2981/P.$$

The P value in the above expressions refers to the spawning stock of females and R symbolizes the production of virgin females 4, 5 and 6 years later. Because each year's run is composed of virgins from three year classes, the numbers of virgin females (R) emanating from a particular year class were assumed to be sexually mature at the following proportions: 23.7 percent at age IV, 70.2 percent at age V and 6.1 percent at age VI. These percentages were used because they are identical to the average values as determined from age compositon data from 1966 - 1977 (Table 27). Though either the Beverton-Holt or the Ricker reproduction models are easily incorporated into the self-regenerating model, the Ricker type was employed in the forthcoming analyses because I believe that it's dome-shaped curve better exemplifies the consequences of density dependent recruitment.

The self-regenerating model is designed to examine changes in the equilibrium size of the female run, equilibrium yield (kg), equilibrium catch in numbers, average weight (kg) of a female shad, percent of repeat spawners, and the equilibrium escapement of female shad at various combinations of natural (M) and fishing (F) mortality during a specified number of generations. Because most female shad attain sexual maturity at age V, the duration of each generation was adjudged to be about 5 years. Thus, for any combination of F and M, 5 generations is equivalent to about 25 years.

The computation begins by using the Thompson-Bell model to determine the eight equilibrium parameters (see page115) at a particular rate of fishing (F) and natural (M) mortality. The equilibrium escapement of female shad (P_t) is then substituted into the Ricker stock-recruitment expression

$$R = P_t e^{0.8586\ (1\ -\ P_{t}/162)}$$

to produce the numbers of mature virgin females (R) to the next generation. The R value is multiplied by the proportions 0.237, 0.702, and 0.061 to obtain the numbers of virgin females at ages IV, V, and VI respectively. The age-specific levels ($R_{IV} - R_{VI}$) of recruitment are reentered into the Thompson-Bell model (equation 27) and the new estimates of the equilibrium parameters are obtained in generation 1. The level of female escapement (P_t) as determined in generation 1 is again reentered into the stock-recruitment model yielding the numbers of virgin female recruits in

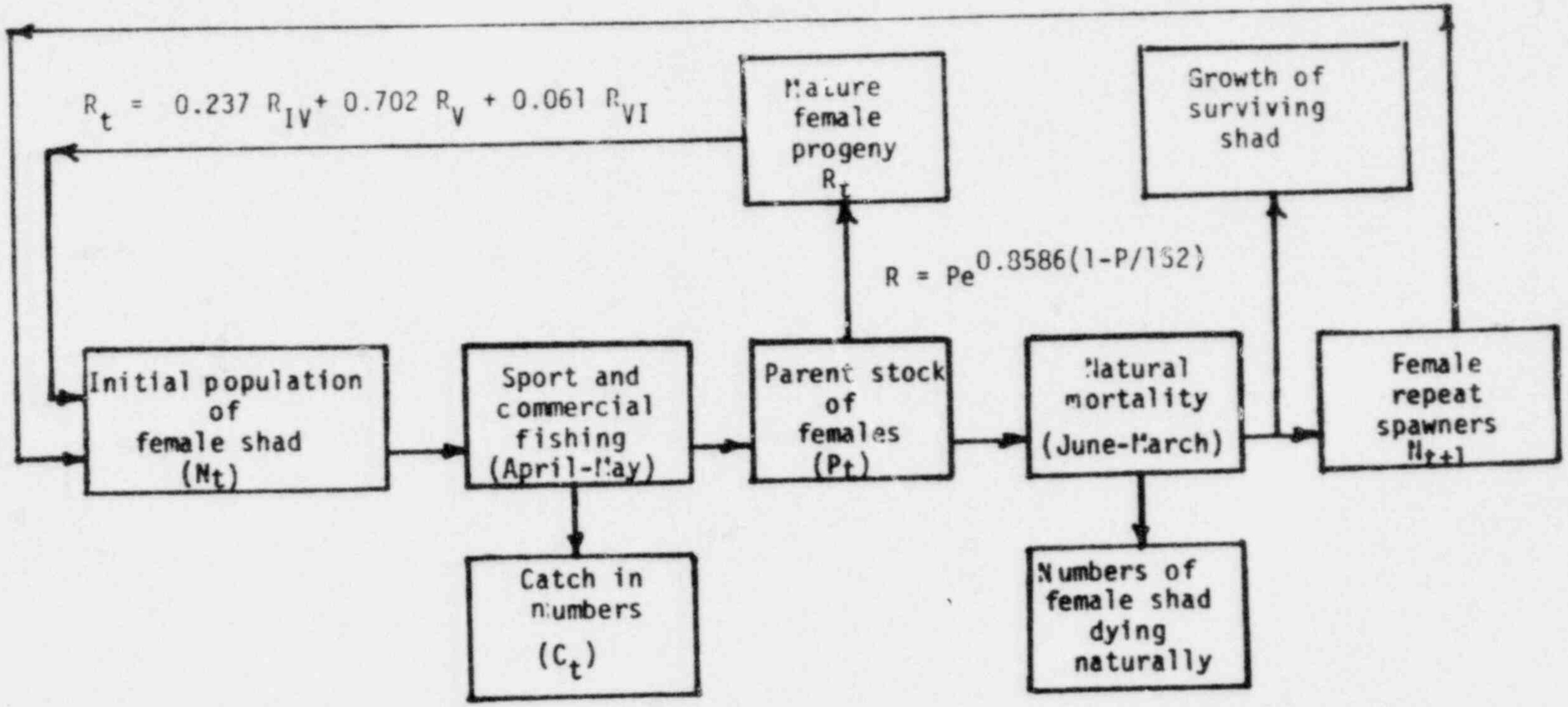

Figure 18. Flow diagram depicting the various biological processes of the self-regenerating model.

generation 2. In the following analyses, the model is permitted to continue through a number of generations either until the size of the shad run and yield reach an equilibrium, or until these parameters approach extinction. The entire program for the model is presented in Appendix 4 , and the various biological processes are illustrated by a flow diagram in Figure 18.

Use of the model is illustrated for four scenarios. The first: equilibrium yield is computed at various combinations of fishing mortality (F from 0.09 to 2.33) each at three levels of natural mortality (M = 0.4, 0.8, and 1.4). The parameters of the Ricker reproductive curve were maintained at the historical (1940 - 1971) level (a = 0.8586, Pr = 162). This scenario depicts the shad fishery from 1940 - 1971 and is identical to that previously evaluated using the Thompson-Bell model (Tables 32 - 37).

The second scenario examines the potential consequences on equilibrium yield of a 50 percent increase in virgin recruitment during the 1980's due to spawning in the Holyoke pool from 1975 and thereafter. Fishing mortality (F) was allowed to vary from 0.09 to 2.33 at a natural mortality rate (M) of 2.0. The higher level of adult natural mortality was employed to reflect substantial post-spawning mortality resulting from entrapment in the canal systems at Holyoke. This is reasonable since from 1975 - 1978 approximately 25 to 60 percent of the parent stock had been transported over Holyoke and since down-stream migrant facilities were not in operation during that period. A 50 percent increase in female recruitment beyond historical levels (1940 - 1971) was achieved by adjusting the parameters of the Ricker equation (a = 1.2648, Pr = 238.6). For further details refer to Appendix 5 .

The third scenario is based on the same circumstances as the second except that virgin recruitment is now allowed to expand by 100 percent beyond historical

Table 41. Estimates of key parameters (Columns 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality (M = 0.4).

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
Initial escapement	Number of generations	u_{total} % of run	F total	Percent of repeat spawners	Predicted size of female run	Yield in numbers	Av. weight of fish (kg)	Yield in kg	Equilibrium escapement	Fishing effort (SFU) at F_{total}	Yield kg/effort	Yield/yield max.	Optimum yield coefficient
313,600	2	9	0.09	60.0	348,800	32,300	2.492	80,500	316,500	411	196	0.339	66.4
253,900	4	17	0.19	54.8	333,200	58,500	2.410	140,900	274,700	868	162	0.595	96.4
209,400	4	24	0.27	50.0	317,900	79,600	2.343	186,400	238,400	1,233	151	0.786	118.7
175,400	2	31	0.37	41.8	281,400	100,000	2.315	231,500	181,400	1,689	137	0.977	133.8**
149,000	3	37	0.46	41.6	279,300	105,800	2.241	237,000	173,500	2,100	113	1.000	113.0*
103,900	2	50	0.69	33.1	211,500	107,200	2.161	231,500	104,300	3,151	73	0.977	71.3
75,500	10	60	0.92	26.3	113,900	69,100	2.107	145,700	44,800	4,201	35	0.615	21.5

* maximum sustainable yield

** optimum yield per SFU

Table 42. Estimates of key parameters (Columns 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality ($M = 0.8$).

(1) Initial escapement	(2) Number of generations	(3) u_{total} % of run	(4) F_{total}	(5) Percent of repeat spawners	(6) Predicted size of female run	(7) Yield in numbers	(8) Ave. weight of fish (kg)	(9) Yield in kg	(10) Equilibrium escapement	(11) Fishing effort (SFU) at F_{total}	(12) Yield (kg)/effort	(13) Yield/yield max.	(14) Optimum yield coefficient
213,600	4	9	0.09	40.9	266,900	24,300	2.245	54,400	242,600	411	132	.316	41.7
183,600	3	17	0.19	37.1	258,500	44,700	2.208	98,600	213,900	868	114	.572	65.2
159,000	3	24	0.27	33.8	247,500	61,100	2.177	133,100	186,400	1,233	108	.772	83.4
138,600	4	31	0.37	30.8	233,700	73,500	2.151	158,100	160,200	1,689	94	.918	86.3**
121,900	3	37	0.46	28.1	216,100	81,000	2.129	172,300	135,200	2,100	82	1.000	82.0*
90,100	5	50	0.69	22.3	157,800	79,400	2.086	165,700	78,400	3,151	53	.962	51.0
68,200	15	60	0.92	17.8	66,200	40,000	2.056	82,200	26,200	4,201	20	.477	9.5

* maximum sustainable yield

** optimum yield per SFU

Table 43. Estimates of key parameters (Columns 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality ($M = 1.4$).

(1) Initial escapement	(2) Number of generations	(3) u_{total} % of run	(4) F_{total}	(5) Percent of repeat spawners	(6) Predicted size of female run	(7) Yield in numbers	(8) Ave. weight of fish (kg)	(9) Yield in kg.	(10) Equilibrium escapement	(11) Fishing effort (SFU) at F_{total}	(12) Yield (kg) effort	(13) Yield/ yield max.	(14) Optimum yield coeffi-cient
163,400	2	9	0.09	22.4	211,200	18,900	2.098	39,700	192,300	411	97	.309	30.0
145,500	2	17	0.19	20.5	204,300	34,800	2.085	72,600	169,500	868	84	.566	47.5
129,900	3	24	0.27	18.6	195,600	47,700	2.072	98,900	147,900	1,233	80	.771	61.7
116,000	3	31	0.37	17.0	183,300	57,100	2.060	117,700	126,200	1,689	70	.918	64.3**
104,200	2	37	0.46	15.5	168,200	62,500	2.050	128,200	105,600	2,100	61	1.000	51.0*
80,400	9	50	0.69	12.3	113,500	56,700	2.032	115,300	56,700	3,151	37	.899	33.3
62,600	20	60	0.92	--	--	--	--	--	--	4,201	--	--	--

* maximum sustainable yield

** optimum yield per SFU

levels. Natural mortality (M) was again maintained at 2.0. The Ricker parameters were altered so as to correspond with a 100 percent increase in virgin recruitment (a = 1.5489, Pr = 292.3). Details for this computation are given in Appendix 5 .

The fourth scenario examines the consequences of a 30 percent decline in the level of female virgin recruitment during the 1980's due to substantial juvenile mortality during emigration from above the Holyoke Dam from 1975 and thereafter. In this scenario, adult natural mortality (M) was maintained at 2.0, and the parameters (a = 0.5003, Pr = 94.4) of the stock-recruitment model were altered so as to conform with a 30 percent decline in virgin recruitment. See Appendix 5 for details.

RESULTS

(a) Scenario 1 - historical recruitment at various rates of natural mortality (M = 0.4, 0.8, 1.4).

Estimates of key parameters for the historical scenario are presented in Columns 1 through 14 of Tables 41 - 43. Given in Column 1 is the initial levels of female escapement as derived from the Thompson-Bell model. Column 2 shows the numbers of generations needed to produce a steady-state condition under various rates of fishing. The parameters in Columns 3 through 14 were previously described in the analyses using the Thompson-Bell model (see pages 118). The single asterisk denotes the level of fishing effort (SFU) which provides a maximum sustainable yield (MSY), whereas a double asterisk denotes the fishing effort (SFU) which results in an optimum yield per SFU.

Results (Tables 41 - 43) reveal that regardless of natural mortality, maximum sustainable yield (MSY) occurs at an annual fishing rate of 37 percent (2100 SFU). When the fishing rate is increased to 50 percent (3151 SFU), equilibrium yield (Column 9) is slightly smaller than that at MSY, but the equilibrium size of the run (Column 6) declines by 24 to 33 percent depending on the level of natural mortality. This signifies the onset of recruitment failure in the shad population. Further increases in the fishing mortality rate to 60 percent (4201 SFU) should generate substantial reductions in both the size of the female run (Column 6) and equilibrium yield (Column 9) within 10 to 15 generations at natural mortality rates (M) of 0.4 and 0.8 (Tables 41 and 42). But at a natural mortality rate of 1.4 (Table 43), the parent stock of females is unable to produce enough recruits to replace the losses at a fishing rate of 60 percent (4201 SFU) due to substantial reduction in the numbers of repeat spawners. As a consequence, the shad run (column 6) and equilibrium yield (Column 9) should proceed enexorably toward zero after some 20 generations. Any increases in fishing to levels greater than 60 percent (4201 SFU) would eventually reduce the shad population to extinction regardless of the natural mortality rate. In reality fishing effort would be likely to stabilize at some level less than 4201 SFU since the economic constraints of increasing costs of fishing effort per unit catch should force many commercial fishermen either to leave the fishery outright, or to greatly curtail their efforts. In addition, an alarming decline in yield and in the size of the run would provoke the management authority into some type of conservation measure.

At the pre 1975 level of natural mortality (M=0.8, Table 42), the results clearly suggest that an annual fishing rate (u_{total}) in excess of 50 percent (3151 SFU) would reduce not only the size of the parent stock (column 6), but perhaps the reproductive capacity of the shad population as well. For instance, by annually removing better than 50 percent of the adult females, the population fecundity would be diminished resulting in a lower probability of good recruitment. A decline in virgin recruitment could ensue in successive generations due to intensive fishing in combination with less than optimal conditions (both biotic and abiotic) prevailing in the river during post-larval and juvenile development. These findings are of particular interest, since they support my previous contention (see pages 35) that heavy fishing pressure during the period 1945-1949 was at least partially instrumental in reducing the size of the shad runs from 1950 - 1955 (Figure 1). Though recruitment failure resulting from overexploitation has not been conclusively demonstrated for any fish population, results from various investigations on marine clupeids are at least consistent with this hypothesis. For example, Murphy (1966) used graphic illustrations and showed that the California sardine, *Sardinops caerulea*, collapsed during the 1950's coincident with heavy fishing. Yokoto (1951) showed similar results for the Japanese sardine, *Sardinops melanosticta*. In the North Sea, Cushing and Bridger (1966) reported that the Atlantic herring, *Clupea harengus*, declined in abundance under heavy fishing pressure from 1955 - 1965. Aside from being clupeids, all of the above fishes are also similar to American shad in that they are fast-growing and short-lived species with low-domed reproductive curves (Cushing, 1973). This suggests that clupeid fishes are particularly vulnerable to recruitment overfishing.

At the present rate of fishing (24 percent) and with increases in natural mortality from 0.8 to 1.4, equilibrium yield (Column 9 Tables 42 and 43) to both the commercial and sport fisheries should decline from 133,100 kg to 98900 kg. This will ensue as a result of the following alterations in the shad population: 1) reduction in the percentage of repeat spawners (Column 5) from 33.8 to 18.6 percent; 2) decline in the equilibrium size of the female run (Column 6) from about 247,500 to 196,600 individuals; and 3) decline in the average weight of a female shad (Column 8) from 2.177 to 2.072 kg. These estimates could become a reality unless the passage of spawners over the Holyoke Dam produces additional numbers of recruits to offset the loss of repeat spawners. Hence, the results of this analysis presents us with the important conclusion that equilibrium yield to the commercial and sport fisheries will decline in magnitude as natural mortality of adult shad increases in dimension.

Though the maximum sustainable yield occurs at a fishing rate of 37 percent (2100 SFU), optimum yield per SFU is achieved by annually harvesting about 31 percent (1689 SFU) of the female run (Tables 41-43). This occurs at all three levels of natural mortality examined (M = 0.4, 0.8, and 1.4). This estimate is smaller than those previously derived from the Thompson-Bell model (Tables 32-37)which exemplifies the danger of using a simple yield model to formulate management policies without knowledge of the stock-recruitment relationship.

If the natural mortality rate had been maintained at levels less than 0.8 (Table 42) commercial fishing effort could have been expanded from the present levels of between 1050 and 1200 SFU to approximately 1689 SFU without undue harm to the shad population. Such a modest expansion of the fishery could have been accomplished by permitting the commercial fishermen to harvest shad for six nights a week rather than for five. This would allow the sport fishery to harvest about 5 percent of the females, and the commercial fishery between 25 and 30 percent, resulting in a sustainable yield of about 158,100 kg (Column 9) and an equilibrium escapement of 160,200 females (Column 10).

It should be noted, however, that the determination of an optimum fishing strategy for Connecticut River shad is presently confounded by the marked reduction in the numbers of repeat spawners during 1976 and 1977. According to this analysis, an increase in natural mortality from 0.8 to 1.4 will generate a 27 percent decline in equilibrium escapement from 160,200 to 126,200 females (Column 19, Tables 42 and 43). Since natural mortality of adult shad has increased in dimension during the period 1974 - 1977 presubably due to substantial spawning from above the Holyoke Dam, it would be prudent not to expand commercial fishing effort beyond the present levels of between 1050 and 1200 SFU until it is clearly shown that virgin recruitment during the 1980's has greatly exceeded the historical (1940 - 1971) estimates. This would ensure an equilibrium escapement of some 147,900 females (Column 10, Table 43) and a sustainable yield (Column 9) of 98,900 kg. Using this management strategy, any apparent reductions in recruitment during the 1980's could not be attributed to excessive fishing.

Scenario 2 - 50 percent increase in recruitment at M of 2.0.

As mentioned previously, this scenario presupposes that virgin recruitment will expand by 50 percent relative during the 1980's as a consequence of substantial spawning from above the Holyoke Dam from 1975 - 1978. The computed parameters for

Table 44. Estimates of key parameters (Column 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality (M = 2.0); virgin recruitment increased by 50 percent.

(1) Initial escapement	(2) Number of generations	(3) u_{total} % of run	(4) F_{total}	(5) Percent of repeat spawners	(6) Predicted size of female run	(7) Yield in numbers	(8) Ave. weight of fish (kg)	(9) Yield in kg	(10) Equilibrium escapement	(11) Fishing effort (SFU)at F_{total}	(12) Yield (kg)/ effort	(13) Yield/ yield max.	(14) Optimum yield coeffici
217,000	4	9	0.09	12.3	269,900	24,000	2.041	48,900	245.900	411	119	.202	24.0
195,700	3	17	0.19	11.3	272,600	46,200	2.034	94,000	226,200	868	108	.389	42.0
176,800	2	24	0.27	10.3	272,900	66,300	2.027	134,400	206,700	1,233	109	.556	60.6
159,900	2	31	0.37	9.3	271,400	84,000	2.022	169,700	187,400	1,689	100	.702	70.2
148,900	3	37	0.46	8.5	267,200	98,800	2.017	199,300	168,400	2,100	95	.824	78.3**
113,700	3	50	0.69	6.8	242,000	120,600	2.006	241,900	121,400	3,151	77	1.000	77.0*
89,800	5	60	0.92	5.4	192,900	115,700	1.997	231,100	77,200	4,201	55	.955	52.5
71,300	12	68	1.14	4.3	105,500	71,700	1.990	142,800	33,700	5,205	27	.590	15.9

* maximum sustainable yield

** optimum yield per SFU

this scenario are depicted in Columns 1 through 14 of Table 44. Results reveal that a 50 percent increase in adult progeny production will modify the fishing rate (Column 3) that produces MSY (denoted by a single asterisk) from 37 percent (2100 SFU) to 50 percent (3151 SFU) due to sizeable increases in virgin recruitment. In addition, by intensifying the level of fishing to 60 percent (4201 SFU), equilibrium yield (Column 9) remains close to that at MSY, but both the female run (Column 6) and equilibrium escapement (Column 10) exhibit a drastic decline in abundance within 5 generations. By annually harvesting some 68 percent (5205 SFU) of the female run, the shad population (Column 6), equilibrium yield (Column 9), and equilibrium escapement (Column 10) should dwindle to dangerously low levels within about 12 generations, and if the fishing rate (Column 3) was expanded to levels greater than 68 percent (5205 SFU), then the shad population would be pushed toward extinction within 5 to 10 generations. Hence it is clear from this analysis that as virgin recruitment increases in magnitude, the shad population becomes better able to tolerate higher levels of exploitation.

According to this analysis, the level of fishing which produces an optimum yield per SFU should increase from the previous level of 31 percent (1689 SFU) to 37 percent (2100 SFU) with a 50 percent increase in recruitment. This will result in an equilibrium yield of 199,300 kg. (Column 9) and an equilibrium escapement of about 168,400 females (Column 10). It should be noted, however, that if adult natural mortality continues at the 1976/1977 level (M = 2.0), then equilibrium yields (Column 9, Table 44) are only slightly greater than those (Column 9, Table 42) at an M of 0.8 even though virgin recruitment may increase by 50 percent. This is due to the inevitable loss in stock biomass resulting from a decline in the numbers of older, repeat spawning females. Thus, to compensate

Table 45. Estimates of key parameters (Columns 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality ($M = 2.0$); virgin recruitment increased by 100 percent.

(1) Initial escapement	(2) Number of generations	(3) u_{total} % of run	(4) F_{total}	(5) Percent of repeat spawners	(6) Predicted size of female run	(7) Yield in numbers	(8) Ave. weight of fish (kg)	(9) Yield in kg	(10) Equilibrium escapement	(11) Fishing effort (SFU) at F_{total}	(12) Yield (kg)/ effort	(13) Yield/ yield max.	(14) Optimum yield coefficient
289,400	6	9	0.09	12.3	328,600	29,200	2.041	59,600	299,400	411	145	.153	22.2
261,000	6	17	0.19	11.2	336,800	57,100	2.034	116,100	279,700	868	134	.298	39.9
235,800	5	24	0.27	10.3	344,100	83,600	2.027	169,400	260,600	1,233	137	.435	59.6
213,300	3	31	0.37	9.3	349,800	108,200	2.022	218,800	241,600	1,689	130	.562	73.1
193,200	3	37	0.46	8.5	352,700	130,500	2.017	263,100	222,200	2,100	125	.676	84.5
151,600	3	50	0.69	6.8	349,800	174,300	2.006	349,600	175,500	3,151	111	.899	99.8**
119,700	4	60	0.92	5.4	324,700	194,800	1.997	389,000	129,900	4,201	93	1.000	93.0*
95,000	5	68	1.14	4.3	268,700	182,800	1.990	363,800	85,900	5,205	70	.935	65.5
75,500	13	74	1.35	3.5	165,600	123,300	1.985	244,600	42,400	6.164	40	.629	25.2

*maximum sustainable yield

** optimum sustainable per SFU

Table 46. Estimates of key parameters (Columns 5 through 14) for the shad population at various levels of fishing (F) and at a constant rate of natural mortality ($M = 2.0$); virgin recruitment declines by 30 percent.

(1) Initial escapement	(2) Number of generations	(3) u_{total} % of run	(4) F_{total}	(5) Percent repeat spawners	(6) Predicted size of female run	(7) Yield in numbers	(8) Ave. weight of fish (kg)	(9) Yield in kg	(10) Equilibrium escapement	(11) Fishing effort (SFU) at F_{total}	(12) Yield (kg)/ effort	(13) Yield/ yield max.	(14) Optimum yield coefficient
200,000	5	9	0.09	12.3	112,300	10,000	2.040	20,300	102,300	411	49	0.481	23.6
200,000	5	17	0.19	11.2	99,800	16,900	2.034	34,400	82,900	868	40	0.815	32.6**
200,000	7	24	0.27	10.3	84,000	20,400	2.028	41,300	63,600	1,233	33	0.979	32.3
200,000	8	31	0.37	9.4	67,400	20,900	2.022	42,200	46,500	1,689	25	1.000	25.0*
200,000	8	37	0.46	8.5	50,900	18,800	2.016	38,000	32,100	2,100	18	0.900	16.2
200,000	12	50	0.69	-	-	-	-	-	-	3,151	-	-	-

* maximum sustainable yield

** optimum yield per SFU

for losses in stock biomass, and to restore equilibrium yield at the pre 1975 levels, progeny production emanating from above the Holyoke Dam must enhance virgin recruitment by at least 50 percent during the 1980's. In the event that virgin recruitment increases in magnitude by 50 percent or more, then the potential exists for an expansion of the commercial fishery from the present levels of between 1050 and 1200 SFU to about 2100 SFU.

Scenario 3 - 100 percent increase in recruitment at an M of 2.0.

The computed parameters for the above conditions are presented in Column 1 through 14 of Table 45. Results indicate that MSY is attained by harvesting about 60 percent (4201 SFU) of the female run, and that optimum yield per SFU occurs at a fishing rate of 50 percent (3151 SFU). Thus by allowing the fishing effort to expand from the present levels of between 1050 and 1200 SFU to about 3151 SFU, equilibrium yield should be about 349,600 kg (Column 9), leaving some 175,000 females (Column 10) to spawn annually.

At the present rate of fishing (24 percent), a 100 percent increase in virgin recruitment will generate an equilibrium yield of about 169,400 kg (Column 9, Table 45) which is 27 percent greater than the 133,100 kg determined for the pre 1975 era (Column 9, Table 42). This clearly represents an optimum situation for any fishery manager, since a 100 percent increase in the level of virgin recruitment during the 1980's would more than compensate for the loss of repeat spawners resulting in great financial benefits for the commercial fishery. In addition, increases in virgin recruitment as stated above would produce sizable increases in the shad runs during the 1980's thereby enabling the population to endure a greater fishing rate.

Scenario 4 - 30 percent decline in recruitment at an M of 2.0.

The computed parameters for this scenario are shown in Columns 1 - 14 of

Table 46. Results clearly demonstrate that a 30 percent decline in female virgin recruitment relative to the historical levels (1940 - 1971) would result in a substantial decline in both equilibrium yield (Column 9) and the size of the shad runs (Column 6) in future years. For instance, MSY of 42,200 kg (Column 9) is attained by annually harvesting 31 percent (1689 SFU) of the female run resulting in an equilibrium escapement of only 46,500 females (Column 10). In contrast, the optimum yield per effort (Column 14) is achieved by annually harvesting 17 percent (868 SFU) of the run resulting in an equilibrium yield of 34,400 kg (Column 9) and an escapement of 82,900 female shad (Column 10).

At the present rate of fishing (u_{total} of 24 percent), equilibrium yield to the commercial and sport fisheries should decline from 133,100 kg (column 9, Table 42) during the pre-1975 era to 41,300 kg (Column 9, Table 46) with a 30 percent decline in virgin recruitment. In addition, the female run is expected to decline in abundance from 247,500 fish (Column 6, Table 42) during the pre-1975 era to 84,000 fish (Column 6,Table 46) under the prescribed conditions. If this scenario becomes a reality during the 1980's, the shad run would decline to between 100,000 and 200,000 shad of both sexes thereby requiring the implementation of stringent conservation measures.

CONCLUSIONS AND RECOMMENDATIONS

It is appropriate at this concluding stage to summarize the results of the self-regenerating model, since these findings should assist in the development of effective fishing strategies for Connecticut River shad. Before continuing, I should emphasize that the intent of the previous analyses was to examine a number of scenarios regarding the fate of the shad runs during the 1980's and to determine for each situation the level of commercial and sport fishing that would provide an adequate spawning stock and the greatest equilibrium yield per SFU. Because the fish lift facility at the Holyoke Dam became fully automated in 1975, a large portion of the 1975 - 1978 year classes had been produced between the Holyoke Dam and the next dam at Turners Falls. Moreover, in 1980, the fishway at Turners Falls will begin operation allowing shad to spawn as far north as the next dam at Vernon, Vermont. Because specific down-stream migrant facilities are presently absent from the Holyoke Dam and not planned for the Turners Falls facility, juveniles produced above Holyoke can emigrate only by passing over the dam, through the turbines, or through a complex canal system. Since no relative index of juvenile abundance (catch/effort) exists for the 1975 - 1978 year classes, it is impossible to determine whether the absence of down-stream facilities at Holyoke had affected the abundance of these year classes. It follows that any indication of recruitment failure can be realized only after these cohorts (1975 - 1978) become sexually mature and enter the fishery after 1979. Hence, the size of the shad runs and the types of management decisions made during the 1980's will largely depend upon whether juvenile mortality during emigration through the Holyoke and Turners Falls facilities had been intense enough to affect the levels of virgin recruitment four and five years later.

Given below is an array of fishing strategies based upon the results (Tables 41 - 46) of the self-regenerating model. Because effective management of Connecticut

River shad is feasible only after the abundance of the 1975 - 1978 year classes has been evaluated, the various fishing strategies presented should not be considered for implementation until those year classes have entered the fishery (i.e. from 1980 - 1983 for female recruits).

Scenario I (Tables 42 - 43) Historical Recruitment (1940 - 1971)

If during the period 1980 - 1983 average female recruitment continues at the historical levels (1940 - 1971) of between 100,000 and 175,000 virgin females, and if adult natural mortality (M) is maintained at a rate of 1.4 or greater, then fishing effort should not be permitted to increase beyond the present levels (1050 - 1200 SFU). This would allow the sport and commercial fishery to annually harvest about 5 and 22 percent, respectively, of the female run resulting in a sustainable yield of 98,900 kg (Column 9, Table 43) and a spawning stock of approximately 147,900 females (Column 10). Although the results (Table 43) of the self-regenerating model indicated that optimum yield per SFU would occur at a fishing rate (u_{total}) of 31 percent (1689 SFU), such an expansion is not recommended because female escapement to the spawning grounds would then decline to about 126,200 individuals (Column 10); a level which I consider inconsistent with the maintenance of an adequate parent stock.

The previous analyses also revealed that at the present fishing rate (u_{total} = 24 percent), an increase in adult natural mortality (M) from the pre 1975 level of 0.8 to the present level of 1.4 or greater should result in a 23 percent reduction in equilibrium yield (from 133,100 kg to 98,900 kg). This projected decline should occur during the 1980's due to sizable reductions in the numbers of older, repeat spawning females resulting from the absence of downstream migrant facilities. The above prediction is based on the assumption that adult natural mortality during the 1980's will remain at the 1975 - 1977 levels. However, if downstream migrant facilities were constructed by 1980 at the Holyoke and Turners Falls Dams, then adult natural mortality could perhaps be restored to the pre 1975 level ($M = 0.8$), thereby enhancing the numbers of repeat spawning females in future years. Under these conditions, it would be appropriate to expand fishing effort to 1689 SFU and annually harvest about 31 percent of the female run. This should result in an equilibrium yield of about 158,100 kg (Column 9, Table 42).

If the above scenario becomes a reality by 1983, one of the following statements regarding reproduction and subsequent recruitment from above Holyoke must be true: 1) ova to juvenile survival from above the dam is similar to that from below, and juvenile mortality resulting from emigration at the Holyoke facility had only a minimal influence upon year class strength; or 2) ova to juvenile survival from above Holyoke is greater than that from below, but juvenile mortality due to emigration at Holyoke was sufficiently high as to offset any increases in year class abundance. Either of these statements would be valid interpretations provided that the formation of year class abundance occurs before the juvenile shad leave the Connecticut River. The significant positive correlation between the juvenile index of abundance for the 1966 - 1972 year classes and the abundance of age V females of the same year class certainly supports the hypotheses (Figure 16).

In summary, if female virgin recruitment from 1980 - 1983 remains at the historical level (1940 - 1971) of between 100,000 and 175,000 virgin females, then fishing effort should not be permitted to increase beyond the present levels (1050 - 1200 SFU). To reduce adult natural mortality, downstream migrant facilities should be constructed by 1980 at Holyoke and Turners Falls. If this project succeeded in restoring natural mortality (M) to the pre 1975 level of 0.8, then it would be appropriate to expand fishing effort to around 1689 SFU thereby permitting both fisheries combined to annually harvest about 31 percent of the female run. I would emphasize, however, that an economic feasibility study should be conducted prior to any proposed expansion of the commercial fishery.

Scenario 2 (Table 44) - 50 percent increase in virgin recruitment

If during the period 1980 - 1983 average female recruitment increases by at least 50 percent relative to the historical levels (100,000 - 175,000 individuals), and if adult natural mortality (M) remains at a level between 1.4 and 2.0, the shad runs should increase by about 10 percent (Column 6, Table 44) relative to the historical runs (Column 6, Table 42). Much greater increases in stock abundance are hindered by substantial losses of repeat spawners resulting from the absence of downstream migrant facilities at Holyoke and Turners Falls. For example, with an increase in adult natural mortality (M) from 0.8 to 2.0, few spawners are allowed to return in the following year thereby reducing both the number of age groups and the average weight of a female shad from 2.177 kg (Column 8, Table 42) to 2.027 kg (Column 8, Table 44). Thus, although the size of the shad runs during the 1980's would be expected to increase slightly following a 50 percent increase in virgin recruitment, the high rate of natural mortality (2.0) would prevent any substantial gains in yield to both fisheries. For example, at the present fishing rate (u_{total} = 24 percent), equilibrium yield (Column 9, Table 44) at a natural mortality rate of 2.0 was computed as 134,400 kg; a level which is only slightly higher than that (133,100 kg) for the pre 1975 era (Column 9, Table 42). Moreover, the annual shad runs should exhibit greater oscillations in abundance because the loss of repeat spawners should produce greater variations in the magnitude of the runs particularly during years when weak year classes enter the fishery. Hence, to mitigate fluctuations in the size of the shad runs, and to restore adult natural mortality (M) to the pre 1975 level of 0.8, the construction of downstream migrant facilities at Holyoke and Turners Falls is essential for management of Connecticut River shad during the 1980's. This should result in greater numbers of repeat spawners, in higher yields to both the commercial and sport fisheries, and in larger and more stable shad runs during future years.

The results (Table 44) of this scenario also indicated that the greatest yield per SFU would occur by annually harvesting about 37 percent of the female run. Thus, if it is economically feasible, fishing effort could be expanded from the present level (1050 - 1200 SFU) to about 2100 SFU without harm to the spawning population. Such an increase in fishing effort should result in an equilibrium yield of 199,300 kg (Column 9, Table 44) leaving some 168,400 female shad (Column 10 to spawn annually.

Scenario 3 (Table 45) - 100 percent increase in virgin recruitment

If during the period 1980 - 1983 average female recruitment should increase in dimension by 100 percent or more relative to the historical levels (100,000 - 175,000 individuals), and if adult natural mortality (M) continues at between 1.4 and 2.0, the shad runs should increase in abundance by about 39 percent (Column 6, Table 45) relative to the pre 1975 levels (Column 6, Table 42). This would occur despite substantial losses of repeat spawners. Moreover, if the annual fishing rate (u_{total}) is maintained at the present level (24 percent), equilibrium yield should expand from the pre 1975 level of 133,100 kg (Column 9, Table 42) to approximately 169,400 kg (Column 9, Table 45). Though substantial post-spawning mortality due to the lack of down-stream facilities would reduce the average weight of a female shad from 2.177 kg (Column 8, Table 42) to about 2.027 kg (Column 8, Table 45), the marked increase in the numbers of virgin females would more than compensate for the loss in stock biomass. Accordingly, the size of the shad runs during the 1980's is expected to vary between 500,000 - 800,000 individuals (both sexes) suggesting that ova to juvenile survival from above Holyoke was excellent and that juvenile mortality resulting from downstream passage had little influence on year class strength. Although the construction of downstream facilities appears unnecessary under these conditions, the loss of repeat spawners would nevertheless result in excessive oscillations in both stock size and yield to the commercial fishery. Thus, even under such optimal conditions, the construction of downstream facilities at Holyoke and Turners Falls is still important for management of Connecticut River shad during the 1980's.

The results (Table 45) of this analysis also indicated that the greatest yield per SFU would occur by annually harvesting about 50 percent of the female run, which would result in an equilibrium yield of 349,600 kg (Column 9, Table 45) and an equilibrium escapement of about 175,500 females (Column 9). Thus, the potential would exist for a major expansion in sport and commercial fishing from the present level (1050 - 1200 SFU) to approximately 3151 SFU.

Scenario 4 (Table 46) - 30 percent reduction in virgin recruitment

If during the period 1980 - 1983 average female recruitment should diminish by 30 percent or more as compared to the historical levels (100,000 - 175,000 individuals), and if adult natural mortality (M) continues at between 1.4 and 2.0, both the size of the female run (84,000 individuals) and the equilibrium yield (41,300 kg) should decline to very low levels. Although this scenario is not expected to occur, it is nevertheless conceivable, since downstream migrant facilities are presently non-existent. Accordingly, in order for juvenile shad to descend from above Holyoke during October and November, they must traverse either over the top of the dam, through the turbines, or through the canal system. It follows that substantial juvenile mortality (e.g. 50 percent or greater) could occur from abrasions in the spillway, pressure changes through the turbines, and to other mechanical injuries. Mechanical injury as described above could either kill the juveniles outright, or greatly weaken them so that they become more vulnerable to predation.

Such a situation presents a very difficult management problem, especially after considering that the formation of year class strength appears to occur before the juveniles leave the Connecticut River. The decline in the shad runs from 1980 and onward would be directly attributed to mortality which had occurred from 1975 - 1978. Moreover, this problem would be complicated further by our inability to detect a decline in year class abundance until the cohort enters the fishery, since no index of juvenile abundance (catch/effort) is available after 1973. Under these conditions, even if the fish-lift facilities at Holyoke and Turners Falls were completely shut-down after 1983, such action would have no immediate impact on the decline because a large proportion of the parent stock from 1979 - 1983 would have already been transported over Holyoke. If juveniles from these year classes suffered intense mortality while descending from above Holyoke, then a decline in shad abundance would persist through 1988. Because we are presently unable to determine whether year class abundance has been influenced by the lack of downstream facilities, management of Connecticut River shad after 1979 will be effective only if it is carefully conceived and sufficiently flexible as to deal with an array of possible situations, particularly the unpleasant ones such as scenario 4. Given below are two management recommendations pertaining to scenario 4 which should be considered for implementation prior to 1981.

First, to ensure the safe passage of juveniles from above Holyoke and Turners Falls, downstream migrant facilities should be constructed by no later than 1980. In addition, similar facilities should be included in the fishway passage facilities at Vernon and Bellows Falls Dams. If the above measures cannot be implemented by the prescribed time periods, then the only other alternative is to regulate the numbers of adult shad annually transported over Holyoke. Beginning in 1980, the numbers of adult shad annually transported should be limited to less than 50,000 fish (both sexes) until 1984, when biologists can evaluate the abundance of virgin adults in the 1975 - 1978 year classes. If the abundance of these year classes is similar to or greater than that from the historical cohorts (1940 - 1971), then the restrictions on passage should be rescinded and full passage reinstated in 1984. Under these conditions, the fishing strategies for scenarios 1 - 3 should be considered for implementation. However, if the shad runs from 1980 - 1983 exhibit a noticeable decline (i.e. less than 200,000 fish of both sexes) in abundance, then this should be construed as evidence of substantial juvenile mortality from 1975 - 1978 due to the absence of downstream facilities. Accordingly, in 1984, further regulations would have to be employed in an effort to ameliorate the situation. Firstly, we should terminate any further passage of adult shad until downstream migrant facilities are constructed at Holyoke and Turners Falls. Secondly, fishing effort pertaining to the commercial and sport fisheries should be reduced from the present levels (1050 - 1200 SFU) to less than 868 SFU to further protect the remaining parent stock. According to the previous analyses (Table 46), both fisheries combined would then harvest about 17 percent of the female run. These additional regulations, in combination with the 50,000 fish restriction at Holyoke from 1980 - 1983, should produce favorable results in 1985 due to the following: 1) greater numbers of virgin females in the 1985 run since most of the 1980 cohort would have been spawned below the Holyoke Dam; and 2) greater numbers of repeat spawners in the 1985 run because no adult shad from the 1984 run would have been permitted to pass over Holyoke. Thus, if restrictions regarding fish passage at Holyoke were employed by 1980, and if declines in the shad runs occurred during the period 1980 - 1983, then the enactment of additional conservation measures should improve the situation by 1985. I recognize that a 50,000 fish restriction on passage of adult shad would undoubtedly cause some political problems. However, if neither of these recommendations are adopted by 1980, and if later we discover that the shad runs have diminished in abundance during the 1980's, the prognosis would be grim; there would be only remnants of a run by 198 and none of the fundamental objectives in fishery management could then be pursued.

The second recommendation involves the development of a juvenile catch effort program to determine an annual index of year class abundance some 5 years before the cohort occurs in the fishery. This monitoring program should be initiated by 1979, and should be conducted annually from July through October. It is essential that the choice of sampling gear and the location of sampling stations be patterned after Marcy's (1976) survey 1966 - 1973, since according to Figure 16, variations in the relative abundance of juveniles for year classes 1966 - 1972 were highly correlated with those of age V females from the same year class. Accordingly, the relative abundance of juveniles derived for year classes 1979 and thereafter will have immediate relevance because these estimates could be compared to those from previous year classes (1966 - 1973). In addition, particular attention should be given to secular changes in catch per effort from August through October, since a sharp increase in juvenile abundance during October may provide evidence of successful emigration from above the Holyoke Dam.

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APPENDIX 1 - COMPUTER PROGRAM USED IN DETERMINING THE STATISTICS OF THE THOMPSON-BELL YIELD MODEL (CASE 1 AND CASE 2)

Computations of equilibrium yield and of all other parameters described were facilitated by use of the Hewlett-Packard 97 Programmable Calculator. All program steps and key entries for the Thompson-Bell model are presented in Tables Ala and Alb, respectively, for constant (Case 1) and age-specific (Case 2) natural mortality. Estimates of annual survival (S) and fishing mortality (u_{total}) were stored in primary memory registers 4 - 7, while average weight (kg) for age groups IV - XI was stored in secondary memories S0 - S7. Age-specific recruitment (age IV - VI) was retained in primary registers 8, 9, and A. Repetitive calculations were performed quickly by employing a sub-routine within the major program (program steps 112 - 129 for Case 1, and steps 112 - 144 for Case 2). For each combinations of F and M, estimates of parameters were accomplished within a few seconds.

Table A1a. Program steps for the Thompson-Bell yield model with constant natural mortality.

Program step	Key entry	Program step	Key entry
001	LBLC	031	P S
002	RCLA	032	X
003	ST+0	033	ST+3
004	ENT	034	RCL 6
005	RCL5	035	ENT
006	X	036	RCLA
007	ST+2	037	X
008	ENT	038	ST+1
009	P S	039	ENT
010	RCL0	040	RCL9
011	P S	041	+
012	X	042	STOA
013	ST+3	043	ST+0
014	RCL4	044	1
015	ENT	045	2
016	RCLA	046	STO I
017	X	047	RCL i
018	ST+1	048	STOD
019	ENT	049	GSBB
020	RCL8	050	1
021	+	051	3
022	STOA	052	STO I
023	ST+0	053	RCL i
024	ENT	054	STOD
025	RCL7	055	GSBB
026	X	056	1
027	ST+2	057	4
028	ENT	058	STO I
029	P S	059	RCL i
030	RC1 1	060	STOD

Program step	Key entry	Program step	Key entry
061	GSBB	096	÷
062	1	097	PRTX
063	5	098	RCL2
064	STO I	099	ENT
065	RCL i	100	RCLO
066	STOD	101	÷
067	GSBB	102	PRTX
068	1	103	RCLO
069	6	104	PRTX
070	STO I	105	RCL1
071	RCL i	106	PRTX
072	STOD	107	RCL2
073	GSBB	108	PRTX
074	1	109	RCL3
075	7	110	PRTX
076	STO I	111	R/S
077	RCL i	112	LBLB
078	STOD	113	RCLA
079	GSBB	114	ENT
080	RCLA	115	RCL7
081	CHS	116	X
082	ST+0	117	ST+2
083	RCL1	118	ENT
084	ENT	119	RCLD
085	RCLO	120	X
086	÷	121	ST+3
087	PRTX	122	RCL6
088	RCLO	123	ENT
089	ENT	124	RCLA
090	RCL2	125	X
091	-	126	STOA
092	PRTX	127	ST+0
093	RCL3	128	ST+1
094	ENT	129	RTN
095	RCL2		

Table A1b. Program steps for the Thompson-Bell yield model with natural mortality (M) increasing by 25 percent following age VI.

Program step	Key entry	Program step	Key entry
001	LBLC	031	P S
002	RCLA	032	X
003	ST+0	033	ST+3
004	ENT	034	RCL6
005	RCL5	035	ENT
006	X	036	RCLA
007	ST+2	037	X
008	ENT	038	ST+1
009	P S	039	ENT
010	RCL0	040	RCL9
011	P S	041	+
012	X	042	STOA
013	ST+3	043	ST+0
014	RCL4	044	1
015	ENT	045	2
016	RCLA	046	STO I
017	X	047	RCL i
018	ST+1	048	STOD
019	ENT	049	GSBB
020	RCL8	050	1
021	+	051	3
022	STOA	052	STO I
023	ST+0	053	RCL i
024	ENT	054	STOD
025	RCL7	055	GSBB
026	X	056	1
027	ST+2	057	4
028	ENT	058	STO I
029	P S	059	RCL i
030	RCL1	060	STOD

Program step	Key entry	Program step	Key entry
061	GSBB	096	÷
062	1	097	PRTX
063	5	098	RCL2
064	STO I	099	ENT
065	RCL i	100	RCL0
066	STOD	101	÷
067	GSBB	102	PRTX
068	1	103	RCL0
069	6	104	PRTX
070	STO I	105	RCL1
071	RCL i	106	PRTX
072	STOD	107	RCL2
073	GSBB	108	PRTX
074	1	109	RCL3
075	7	110	PRTX
076	STO I	111	R/S
077	RCL i	112	LBLB
078	STOD	113	RCLA
079	GSBB	114	ENT
080	RCLA	115	RCL7
081	CHS	116	X
082	ST+0	117	ST+2
083	RCL1	118	ENT
084	ENT	119	RCLD
085	RCL0	120	X
086	÷	121	ST+3
087	PRTX	122	RCL6
088	RCL0	123	ENT
089	ENT	124	RCLA
090	RCL2	125	X
091	-	126	STOA
092	PRTX	127	ST+0
093	RCL3	128	ST+1
094	ENT	129	RCLE
095	RCL2	130	ENT

Program step	Key entry
131	1
132	.
133	2
134	5
135	X
136	STOE
137	ENT
138	RCLB
139	+
140	CHS
141	e^x
142	STO6
143	R/S
144	RTN

APPENDIX 2 - METHODS USED TO CALCULATE THE PARAMETERS OF THE RICKER STOCK-RECRUITMENT CURVE.

The emperical curve of stock-recruitment using the Ricker model was estimated by linear regression of $\log_{10}$ (R/P) against P (Columns 5 and 1, Table A2). The slope (0.0023) and y-axis intercept (0.3418) were then converted to natural logarithms (loge):

$$0.0023/0.4343 = 0.0053$$

$$0.3418/0.4343 = 0.7870.$$

The parent stock at replacement (Pr) was estimated using the expression

$$0.7870/0.0053 = 148.5.$$

Given extimates of parameters (a=0.7870 and Pr = 148.5), the equation of stock-recruitment is

$$R = Pe^{0.7870\,(1 - P/148.5)},$$

where R = predicted level of female virgin recruitment (Column 6, Table 3A)

P = size of female parent stock (Column 1).

Because recruitment values shown in Column 6 were derived by logarithms and thus are geometric means, it was necessary to transform those values to the arithmetic scale (Ricker, 1975, p. 175) by utilizing the following expression:

$$\log_{10}\,(AM/_{GM}) = 1.1518s^2 \quad (N-1)/N$$

where GM = geometric values of recruitment (Column 6, Table A3)

AM = arithmetic values of recruitment

s^2 = variance of the linear regression of $\log_{10}$ (R/P) on P

N = sample size.

By substituting my values into the above expression, the following information is obtained:

$$\log_{10}\,(AM/_{GM}) = 1.1518\ (0.0283) \quad 31/32 \;= 0.0316,$$

so that

$$\log_{10} (AM/_{GM}) = 0.0316,$$

and $$AM/_{GM} = 1.075.$$

All the geometric values (Column 6) were multiplied by the quantity 1.075 so as to obtain estimates of the arithmetic means (Column 7). Parameters (a) and (Pr) were then recomputed by linear regression, and the final equation became:

$$R = Pe^{0.8586(1 - P/162)}.$$

Table A2. Calculations for the Ricker stock-recruitment curve.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Year	Parent (P) X 1000	$Log_{10}(P)$	Progeny (R) X 1000	$Log_{10}(R)$	$Log_{10}(R/P)$	R(X 1000)	Adjusted[1/] R (X 1000)
1940	212	2.326	193	2.286	-0.040	151	162
1941	284	2.453	188	2.274	-0.179	139	149
1942	237	2.375	156	2.193	-0.182	148	159
1943	229	2.360	135	2.130	-0.230	150	161
1944	200	2.301	113	2.053	-0.248	153	164
1945	123	2.090	88	1.944	-0.146	140	151
1946	101	2.004	103	2.013	0.009	130	140
1947	75	1.875	129	2.111	0.236	111	119
1948	86	1.934	114	2.057	0.123	120	129
1949	75	1.875	97	1.987	0.112	111	119
1950	65	1.813	80	1.903	0.090	101	109
1951	89	1.949	85	1.929	-0.020	122	131
1952	120	2.079	128	2.107	0.028	140	150
1953	74	1.869	163	2.212	0.343	110	118
1954	77	1.887	166	2.220	0.333	113	121
1955	59	1.771	169	2.228	0.457	95	102
1956	73	1.863	169	2.228	0.365	109	117
1957	138	2.140	157	2.196	0.056	146	157
1958	151	2.179	123	2.090	-0.089	149	160
1959	149	2.173	119	2.076	-0.097	149	160
1960	154	2.188	133	2.124	-0.064	150	161
1961	149	2.173	129	2.111	-0-062	149	160
1962	135	2.130	125	2.097	-0.033	145	156
1963	84	1.924	105	2.021	0.097	118	127
1964	101	2.004	112	2.049	0.045	130	140
1965	130	2.114	138	1.140	0.026	143	154
1966	121	2.083	144	2.158	0.075	140	150
1967	133	2.124	109	2.037	-0.087	144	155
1968	100	2.000	111	2.045	0.045	129	139
1969	115	2.061	128	2.107	0.046	138	148
1970	160	2.204	168	2.225	0.021	151	162
1971	160	2.204	227	2.356	0.152	151	162

Table A2. continued

Initial regression equation

correlation coefficient $(r) = -0.7541$

slope $(b) = 0.0023$

y-axis intercept $(a) = 0.3418$

variance $s^2 = 0.0283$

Transform to natural logorithms

$0.0023/0.4343 = 0.0053$

$a = 0.3418/0.4343 = 0.7870$

$Pr = 0.7870/0.0053 = 148.5$

Initial equation

$$R = Pe^{0.7870\ (1-P/148.5)}$$

Final equation

$$R = Pe^{0.8586(1-P/162)}$$

1/ R(Column 6) times 1.075

APPENDIX 3 - METHODS USED TO CALCULATE THE PARAMETERS OF THE BEVERTON-HOLT STOCK-RECRUITMENT CURVE.

The stock-recruitment curve for the Beverton-Holt model was determined by linear regression of P/R (Column 3, Table A3) on P (Column 1). The slope (0.00515) and y-axis intercept (0.3145) were then used in the Beverton-Holt equation:

$$R = {}^{1}/_{0.00515+0.3145/P}$$

where R = predicted level of female recruitment (Column 4, Table A4)

P = size of parent stock (Column 1).

The sum of predicted levels of recruitment (sum of Column 4) is 4081 which is 5.5 percent smaller than observed (4304) levels (sum of Column 2). This occurs because the fraction ($P/_R$) provides harmonic means which are known to be less than arithmetic values. As a consequence, to transform these values (Column 4) to the arithmetic scale, each datum was multiplied by a weighted factor of 1.055 (${}^{4304}/_{4081} = 1.055$). Arithmetic estimates of recruitment are presented in Column 5, and adjusted P/R values are given in Column 6. The final equation:

$$R = {}^{1}/_{0.0048 + 0.2981/P},$$

was determined by linear regression of adjusted P/R (Column 6) on P (Column 1).

Table 3A. Calculations for the Beverton-Holt stock-recruitment curve.

	(1)	(2)	(3)	(4)	(5)	(6)
Year	Parent (P) X 1000	Progeny (R) X 1000	$P/_R$	Predicted R	Adjusted[1/] R	Adjusted $P/_R$
1940	212	193	1.098	151	159	1.333
1941	284	188	1.511	160	169	1.680
1942	237	156	1.519	154	163	1.454
1943	229	135	1.696	153	161	1.422
1944	200	113	1.770	149	157	1.274
1945	123	88	1.398	130	137	0.898
1946	101	103	0.981	121	128	0.789
1947	75	129	0.581	107	113	0.664
1948	86	114	0.754	113	119	0.723
1949	75	97	0.773	107	113	0.664
1950	65	80	0.813	100	106	0.613
1951	89	85	1.047	115	122	0.730
1952	120	128	0.938	129	136	0.882
1953	74	163	0.454	106	112	0.661
1954	77	166	0.464	108	114	0.675
1955	59	169	0.349	96	101	0.584
1956	73	169	0.432	106	112	0.652
1957	138	157	0.879	135	142	0.972
1958	151	123	1.228	138	146	1.034
1959	149	119	1.252	138	146	1.021
1960	154	133	1.158	139	147	1.048
1961	149	129	1.155	138	146	1.021
1962	135	125	1.080	134	141	0.957
1963	84	105	0.800	112	118	0.712
1964	101	112	0.902	121	128	0.789
1965	130	138	0.942	132	139	0.935
1966	121	144	0.840	129	136	0.890
1967	133	109	1.220	133	140	0.950
1968	100	111	0.901	120	127	0.787
1969	115	128	0.898	127	134	0.858
1970	160	168	0.952	140	148	1.081
1971	160	227	0.705	140	148	1.081
		4,304		4,081		

Table 3A continued

Initial equation:

correlation coefficient (r) = 0.803

slope (b) = 0.000515

y-axis intercept (a) = 0.3145

$R = {}^{1}/_{0.00515+0.3145/P}$

Final (adjusted) equation:

r = 0.803

b = 0.00488

a = 0.2981

$R = {}^{1}/_{0.00488+0.2981/P}$

1/ adjusted R = predicted R(1.055),
where $1.055 = 4304/_{4081}$

APPENDIX 4 - COMPUTOR PROGRAM USED IN DETERMINING THE STATISTICS OF THE SELF-REGENERATING MODEL.

Computations of parameters from the self-regenerating model were performed on the Hewlett-Packard 97 Programmable Calculator. All program steps and key entries are presented in Table A4. The Ricker stock-recruitment parameters (a) and (Pr), respectively,were substituted into program steps 4 - 6 and 11 - 15. Virgin female shad for each year class was assumed to attain sexual maturity at the following proportions: 0.237 at age IV, 0.702 at age V, and 0.061 at age VI. These values were inserted into program steps 22 - 25, 29 - 32, and 36 - 39, respectively. The parameters of growth (weight-age), fishing mortality (u_{total}) and survival (S) were stored in primary and secondary memory registers. All calculations for age groups VI - XI were facilitated by employing a sub-routine within the major program (program steps 161 - 178). The numbers of female shad escaping to spawn (P_t) were determined for each generation and stored in primary memory register C. This value (P_t) was later recalled from program memory and looped back (GTOC) to the beginning of the program, producing the numbers of virgins (P) and all parameters in generation 2. The entire program scheme is self-regenerating and will continue indefinitely until it is halted manually by a return command (RTN).

Table A4. Program steps for the self-regenerating yield model.

Program step	Key entry	Program step	Key entry
001	LBLC	031	0
002	RCLC	032	2
003	PRTX	033	X
004		034	STO8
005	P/	035	RCLB
006		036	.
007	÷	037	0
008	CHS	038	6
009	1	039	1
010	+	040	X
011		041	STO9
012		042	RCLA
013	a	043	ST+0
014		044	ENT
015		045	RCL5
016	X	046	X
017	e^x	047	ST+2
018	RCLC	048	ENT
019	X	049	P S
020	PRTX	050	RCL0
021	STOB	051	P S
022	.	052	X
023	2	053	ST+3
024	3	054	RCL4
025	7	055	ENT
026	X	056	RCLA
027	STOA	057	X
028	RCLB	058	ST+1
029	.	059	ENT
030	7	060	RCL8

Table A4. continued

Program step	Key entry	Program step	Key entry
061	+	096	1
062	STOA	097	4
063	ST+0	098	STO I
064	ENT	099	RCL i
065	RCL7	100	STOD
066	X	101	GSBB
067	ST+2	102	1
068	ENT	103	5
069	P S	104	STO I
070	RCL1	105	RCL i
071	P S	106	STOD
072	X	107	GSBB
073	ST+3	108	1
074	RCL6	109	6
075	ENT	110	STO I
076	RCLA	111	RCL i
077	X	112	STOD
078	ST+1	113	GSBB
079	ENT	114	1
080	RCL9	115	7
081	+	116	STO I
082	STOA	117	RCL i
083	ST+0	118	STOD
084	1	119	GSBB
085	2	120	RCLA
086	STO I	121	CHS
087	RCL i	122	ST+0
088	STOD	123	ST+1
089	GSBB	124	RCL1
090	1	125	ENT
091	3	126	RCL0
092	STO I	127	÷
093	RCL i	128	PRTX
094	STOD	129	RCL0
095	GSBB	130	ENT

Table 4A. continued

Program step	Key entry	Program step	Key entry
131	RCL2	155	STO1
132	-	156	STO2
133	PRTX	157	STO3
134	STOC	158	SPC
135	RCL3	159	GTOC
136	ENT	160	RTN
137	RCL2	161	LBLB
138	÷	162	RCLA
139	PRTX	163	ENT
140	RCL2	164	RCL7
141	ENT	165	X
142	RCL0	166	ST+2
143	÷	167	ENT
144	PRTX	168	RCLD
145	RCL0	169	X
146	PRTX	170	ST+3
147	RCL1	171	RCL6
148	PRTX	172	ENT
149	RCL2	173	RCLA
150	PRTX	174	X
151	RCL3	175	STOA
152	PRTX	176	ST+0
153	0	177	ST+1
154	STO	178	RTN

APPENDIX 5. COMPUTATION FOR RICKER PARAMETERS (a) AND (Pr) FOR SCENARIOS 2 - 4.

The computations for determining Ricker parameters (a) and (Pr) in scenarios 2 - 4, respectively, are shown in Tables A5 - A7. Estimates of parent stock (P) in Column 1 were chosen arbitrarily and substituted into the Ricker stock-recruitment equation for the historical scenario (1940 - 1971),

$$R = Pe^{0.8586(1-P/162)},$$

yielding the estimates of female virgin recruitment (R) in column 2. By multiplying R values by 1.5, 2.0, and 0.7, respectively, estimates of virgin recruitment (R) were computed for scenarios 2 - 4 (Column 3, Tables A5 - A7). Estimates of parent stock (Column 1) were then regressed against $\log_{10}$ (R/P) to provide estimates of parameters (a) and (Pr) in the respective scenarios.

Table A5. Calculation of Ricker parameters for scenario 2.

(1)	(2)	(3)	(4)	(5)	(6)
P Female parent stock	$R^{1/}$ Female recruitment	R + 50% (R)	$\log_{10}$ (P)	$\log_{10}$ (R + 50%)	$\log_{10}$ (R + 50%)/$_P$
10	22.4	33.6	1.00	1.53	0.53
30	60.4	90.6	1.48	1.96	0.48
50	90.6	135.9	1.70	2.13	0.43
75	119.0	178.5	1.88	2.25	0.38
100	139.0	208.5	2.00	2.32	0.32
125	152.2	228.3	2.10	2.36	0.26
150	160.0	240.0	2.18	2.38	0.20
175	163.5	245.3	2.24	2.39	0.15
200	163.7	245.6	2.30	2.39	0.09
225	161.4	242.1	2.35	2.38	0.03
250	157.0	235.5	2.40	2.37	-0.03
275	151.3	227.0	2.44	2.36	-0.08
300	144.6	216.9	2.48	2.34	-0.14

Linear regression

P(Column 1) against $\log_{10}$ (R + 50%)/$_P$ Column 6

slope (b) = 0.0023

y-axis intercept (a) = 0.5493

Change to natural logarithm (loge)

$0.5493/_{0.4343} = 1.2648$

$0.0023/_{0.4343} = 0.0053$

Ricker parameters

a = 1.2648

$Pr = 1.2648/_{0.0053} = 238.6$

Final equation:

$$R = Pe^{1.2648(1-P/_{238.6})}$$

1/ $R = Pe^{0.8586(1-P/162)}$

Table A6. Calculation of Ricker parameters for scenario 3.

(1)	(2)	(3)	(4)	(5)	(6)
P Female parent stock	R[1/] Female recruitment	R + 100% (R)	$\log_{10}$ (P)	$\log_{10}$ (R + 100%)	$\log_{10}$ (R + 100%)/$_p$
10	22.4	44.8	1.00	1.65	0.65
30	60.4	120.8	1.48	2.08	0.60
50	90.6	181.2	1.70	2.26	0.56
75	119.0	238.0	1.88	2.38	0.50
100	139.0	278.0	2.00	2.44	0.44
125	152.2	304.4	2.10	2.48	0.39
150	160.0	320.0	2.18	2.51	0.33
175	163.5	327.0	2.24	2.51	0.27
200	163.7	327.4	2.30	2.52	0.21
225	161.4	322.8	2.35	2.51	0.16
250	157.0	314.0	2.40	2.50	0.10
275	151.3	302.6	2.44	2.48	0.04
300	144.6	289.2	2.48	2.46	-0.02

Linear regression

P(Column 1) against $\log_{10}$ (R + 100%)/$_p$ Column 6

slope (b) = 0.0023

y-axis intercept (a) = 0.6727

Change to natural logarithm (loge)

0.6727/0.4343 = 1.5489

0/0023/0.4343 = 0.0053

Ricker parameters

a = 1.5489

Pr = 1.5489/0.0053 = 292.3

Final equation:

$$R = Pe^{1.5489(1-P/292.3)}$$

[1/] $R = Pe^{0.8586(1-P/162)}$

Table A7. Calculation of Ricker parameters for scenario 4.

(1) P Female parent stock	(2) R Female recruitment	(3) R - 30% (R)	(4) $\log_{10}$ P	(5) $\log_{10}$ (R - 30%)	(6) $\log_{10}$ (R - 30%)/$_P$
10	22.4	15.7	1.00	1.20	0.20
30	60.4	42.3	1.48	1.63	0.15
50	90.6	63.4	1.70	1.80	0.10
75	119.0	83.3	1.88	1.92	0.04
100	139.0	97.3	2.00	1.99	-0.01
125	152.2	106.5	2.10	2.03	-0.07
150	160.0	112.0	2.18	2.05	-0.13
175	163.5	114.5	2.24	2.06	-0.18
200	163.7	114.6	2.30	2.06	-0.24
225	161.4	113.0	2.35	2.05	-0.30
250	157.0	109.9	2.40	2.04	-0.36
275	151.3	105.9	2.44	2.02	-0.42
300	144.6	101.2	2.48	2.01	-0.47

Linear regression

P(Column 1) against $\log_{10}$ (R-30%)/$_P$

slope (b) = 0.0023

y-axis intercept (a) = 0.2173

Change to natural logarithm (loge)

0.2173/0.4343 = 0.5003

0.0023/0.4343 = 0.0053

Ricker parameters

a = 0.5003

Pr = 0.5003/0.0053 = 94.4

Final equation:

$R = Pe^{0.5003(1-P/94.4)}$

1/ $R = Pe^{0.8586(1-P/162)}$