POPULATION AND FISHERY CHARACTERISTICS OF GULF MENHADEN, *BREVOORTIA PATRONUS*

WALTER R. NELSON[1] AND DEAN W. AHRENHOLZ[2]

ABSTRACT

Landing data from 1964 to 1978 for the purse seine fishery in the north-central Gulf of Mexico for gulf menhaden, *Brevoortia patronus*, were analyzed to determine growth rate, yield-per-recruit and spawner-recruit relationships, and maximum sustainable yield (MSY). Estimates of stock size, year-class size, and rates of fishing were obtained from cohort analysis. The fishery is characterized by high rates of both fishing and natural mortality. During the period studied, an average of 40% of the population of age-1 and older fish were taken by the fishery and 47% was lost to other causes annually. Although there was substantial scatter about the fitted curve, a Ricker-type spawner-recruit relationship was found to be suitable. The number of age-1 recruits fluctuated annually between 7.5 and 25.4 billion during the period studied. Maximum biomass of a year class is reached at an age of about 1.5 years. Yield-per-recruit estimates were obtained for an array of fishing mortalities and ages of entry. A deterministic simulation model incorporating growth, the spawner-recruit relationship, and age-specific rates of fishing provided an estimate of MSY at 585,118 t with 127% of the current mean rate of fishing. Implications for the current and future status of this fishery are discussed.

Gulf menhaden, *Brevoortia patronus*, are filter-feeding, surface-schooling clupeids that are subjected to an intensive purse seine fishery in the northern Gulf of Mexico. Although annual landings have fluctuated, there has been a general increase since the inception of the modern fishery in 1946 to a high of 820,000 metric tons (t) in 1978. The fishery consists of about 80 refrigerated vessels serving 11 reduction plants at 6 ports in Mississippi and Louisiana. The fishing season is currently set by State law from mid-April to mid-October. Although a majority of the catch is taken off Louisiana and Mississippi, vessels range west into eastern Texas coastal waters and east to the coastal waters of the Florida panhandle. Vessels, aided by spotter aircraft, land from 6,000 to 10,000 t/6-mo fishing season. Excellent background information and descriptions of the fishery have been published by Christmas and Etzold (1977) and Nicholson (1978).

Considerable literature exists on the general biology of gulf menhaden (Reintjes et al. 1960; Reintjes 1964; Reintjes and Keney 1975; Christmas and Etzold 1977); however, information is scarce on the population dynamics of gulf menhaden and on the dynamics and impact of the fishery. Chapoton (1972) and Schaaf (1975a) estimated maximum sustainable yield (MSY). Ahrenholz (1981) described recruitment patterns and estimated natural and fishing mortality rates from returns of tagged juvenile and adult menhaden.

Gulf menhaden have a life history similar to many other estuarine-dependent coastal species. Spawning takes place in coastal and offshore waters in the winter (Christmas and Waller 1975[3]; Lewis and Roithmayr 1981). Larvae move onshore into Gulf estuaries in winter and early spring, transform to juveniles, and remain in the nursery areas until the following fall. Juveniles move offshore during the winter and back into coastal waters the following summer. Spawning occurs for the first time at the end of their second year.

A joint State-Federal-Industry plan developed for gulf menhaden identified the lack of a reliable measure of effective effort and questionable MSY estimates as major concerns in evaluating the gulf menhaden stock and fishery (Christmas and Etzold 1977). Problems encountered in determining the status of gulf menhaden stocks and estimating a long-term yield from catch-effort data on schooling species subjected to a purse seine fishery are compounded by the "dynamic aggregation process" described by Clark and Mangel (1979). Basically, they

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC; present address: Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

[2]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

[3]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr., 20 p. Gulf Coast Research Laboratory, Ocean Springs, MS 39564.

Manuscript accepted July 1985.
FISHERY BULLETIN: VOL. 84, NO. 2, 1986.

hypothesized that surface schooling species are more susceptible to fishing effort than nonschooling species, and indicators of abundance such as catch and catch per unit effort (CPUE) are not reliable when the "intrinsic schooling rate is greater than the intrinsic (population) growth rate". Thus, severe stock depletion could occur in the gulf menhaden fishery before indications of such a situation were evident from catch and CPUE data. The dynamic aggregation process may be further aggravated when the vessels are assisted by spotter aircraft which greatly reduce search time.

We have attempted to estimate characteristics of the gulf menhaden stock, such as population size, biomass, growth rate, spawner-recruit relationship, and to determine characteristics of the fishery, such as fishing mortality, catchability coefficient, yield-per-recruit, equilibrium yield levels, and MSY. These characteristics were determined through application of cohort analysis, yield-per-recruit and spawner-recruit models, and a deterministic simulation model of the Gulf of Mexico population and fishery. Our overall objectives are to evaluate the status of the gulf menhaden stock, determine the impact of the fishery, and provide an outlook for the stock and fishery for resource managers and the purse seine fishing industry in the Gulf of Mexico.

GULF MENHADEN DATA BASE

The National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) has maintained a sampling program for gulf menhaden since 1964. Details of the sampling methodology are given by Nicholson (1978) and Huntsman and Chapoton (1973), and a description of the aging technique is provided by Nicholson and Schaaf (1978). Vessel landings by trip have been recorded, along with pertinent data on vessel size and characteristics. Overall summaries of landings by year and nominal effort (measured in vessel-ton-weeks) are available back to 1945, but the basis for the bulk of this analysis is the catch and effort data (1964-79) and estimated number of fish landed at age for these years (Table 1).

WEIGHT-LENGTH RELATIONSHIP AND GROWTH

Estimates of growth rate are needed for yield analyses and estimates of size at age are needed to determine the spawner-recruit relationship. Although some calculations use length and others weight, all growth estimates were calculated for length, and when required, weight was estimated from the weight-length relationship.

For each age group, there was no major systematic variation in the mean length over the 15 yr period (Fig. 1). In addition, no density-dependent correlations were detectable for mean length at age on stock size or on year-class size, estimated from the subsequent cohort analysis. Hence there appeared to be little, if any, potential gain in estimate accuracy by computing and using year-class specific growth rates when reconstructing the historical population biomass and average size at age for the subsequent spawner-recruit analysis, or to incorporate a density-dependent growth function in the subsequent population simulations for total yield.

Estimates of overall mean length at age for each quarter for the year classes that had passed com-

TABLE 1.—Catch, effort, and estimated number of gulf menhaden landed at age for the 1964-79 fishing seasons (1964-78 for number at age).

Year	Catch (metric tons × 10^3)	No. of vessels[1]	Effort (vessel-ton-weeks × 10^3)	Number at age × 10^6: 0	1	2	3	4	Total
1964	409.4	76	272.9	6.3	3,135.6	1,365.2	108.1	3.9	4,619.1
1965	463.1	82	335.6	46.6	4,888.1	966.3	69.9	1.5	5,972.4
1966	359.1	80	381.3	46.8	3,126.8	850.2	30.5	0.5	4,054.8
1967	317.3	76	404.7	18.7	4,129.2	309.9	10.5	—	4,468.3
1968	373.5	69	382.3	35.4	3,311.5	850.0	27.0	0.2	4,224.1
1969	523.7	72	411.0	10.8	5,766.8	1,011.1	30.4	—	6,819.1
1970	548.1	73	400.0	49.2	3,256.4	2,197.2	34.4	—	5,537.2
1971	728.2	82	472.9	25.3	5,763.3	1,838.1	166.2	3.7	7,796.6
1972	501.7	75	447.5	17.6	3,146.3	1,615.6	68.7	4.4	4,852.6
1973	486.1	65	426.2	57.2	3,012.4	1,082.7	108.2	1.3	4,261.8
1974	578.6	71	485.5	20.0	3,747.3	1,399.0	60.2	—	5,226.5
1975	542.6	78	536.9	96.4	2,512.3	1,453.1	428.2	0.8	4,490.8
1976	561.2	81	575.9	1.8	4,517.7	1,273.1	190.2	—	5,982.8
1977	447.1	80	532.7	1.6	4,800.2	1,209.6	104.3	7.3	6,123.0
1978	820.0	80	574.3	0.0	6,784.7	2,578.8	48.3	3.6	9,415.4
1979	777.9	77	533.9	—	—	—	—	—	—

[1]Includes only vessels that fished 9 or more weeks.

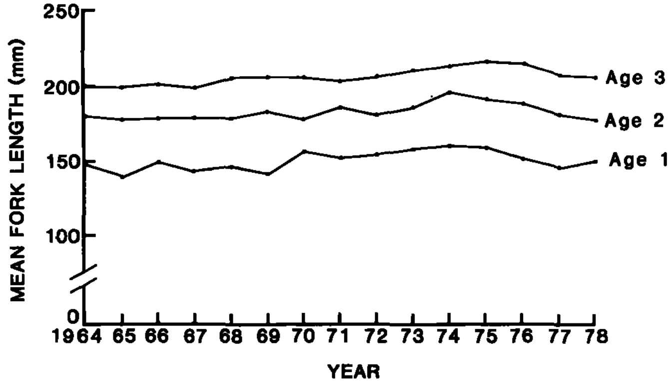

FIGURE 1.—Mean length of gulf menhaden at ages 1-3 taken from commercial landing samples (April-June), 1964-78.

pletely through the fishery were used in the growth computations (Table 2). The von Bertalanffy growth-in length equation

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

where l_t = fork length (mm) at time t (years),
L_∞ = theoretical length at t = infinity (asymptote),
K = growth coefficient,
t_0 = theoretical age when length = 0

was fitted to the data by the computer program BGC3 (Abramson 1971). Although the data points appear stepped between whole age units, they are reasonably well described by the fitted curve (Fig. 2).

TABLE 2.—Mean length and number of fish sampled at age from 1963 to 1974 year classes of gulf menhaden.

Age	Mean fork length (mm)	Number
1.125	121.7	59
1.375	148.3	43,284
1.625	160.5	57,286
1.875	161.3	1,538
2.125	—	—
2.375	182.9	16,687
2.625	190.6	16,452
2.875	194.4	260
3.125	—	—
3.375	210.5	1,063
3.625	216.4	1,368
3.875	220.2	14
4.125	—	—
4.375	227.8	16
4.625	227.5	32
4.875	—	—

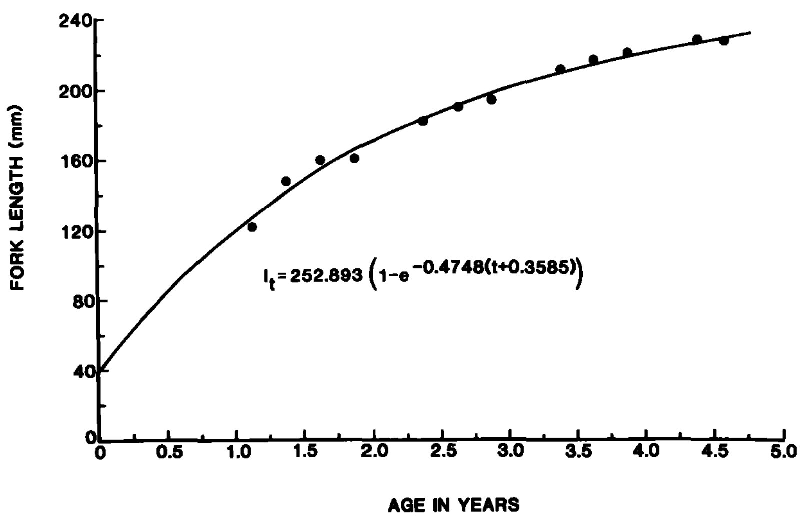

FIGURE 2.—Von Bertalanffy growth curve fitted to average length at age data for gulf menhaden sampled from commercial landings, 1963-74 year classes.

Weight-length regression coefficients were calculated for each of three 2-mo intervals for the major portion of the fishing season for each year class, 1960-77. No systematic variation in the parameter estimates was apparent within years by 2-mo intervals, so the data were pooled between seasons and years. An overall weight-length relationship was obtained from a GM-functional regression (Ricker 1973) on the pooled data. The results are

$$\log_e w = 3.2669 \log_e l - 12.1851 \quad (2)$$

where w = weight in g, and
l = fork length in mm.

The correlation coefficient (r) was 0.976 and the sample size was 168,397.

COHORT ANALYSIS

Estimates of mortality rates and population sizes were obtained by using the Cohort Analysis technique developed by Murphy (1965) and later modified by Tomlinson (1970). Calculations were made with the computer program MURPHY (Tomlinson 1970). This technique does not involve estimates of CPUE. The backward estimation procedure was used. Since the catch equations and general method of application are given in Tomlinson's paper, discussion here will be limited to the source and nature of input data and parameters.

The calendar year was divided into four periods (quarters) of approximately equal length:

Quarter 1 = 1 January to 3 April,
Quarter 2 = 4 April to 3 July,
Quarter 3 = 4 July to 3 October,
Quarter 4 = 4 October to 31 December.

Numbers of fish at each age landed quarterly were sums of weekly estimates obtained by sampling methods outlined by Nicholson (1978). Annual summaries of these data were given earlier (Table 1).

An estimate of the annual rate of instantaneous natural mortality (M) was obtained from an analysis of mark-recapture data (Ahrenholz 1981). M, equal to 1.1 (0.275 per quarter), was assumed to be constant for all ages and seasons.

Because backward sequential computations, using a range of trial estimates of input F (instantaneous fishing mortality) for the oldest age, tend to converge on the correct value of F for the youngest and forward calculations tend to diverge (unless true starting values are used), it is desirable to begin with the oldest age for which reliable landing data are available (Ricker 1975). Because of aging difficulties (Nicholson and Schaaf 1978), we assumed that catch estimates of older fish, mainly age 4, were not reliable, hence for most year classes estimates of the annual rate of instantaneous fishing mortality (F) for age-2 fish were derived from catches of age 2 and age 3 from

$$F_n = (\log_e C_n - \log_e C_{n+1}) - M \quad (3)$$

where C = annual catch in numbers at age (n) from a given cohort.

Initial starting values of F for the oldest age group landed in a year class were adjusted by trial and error until the sum of the quarterly F's for age-2 fish were virtually equal to the estimate of annual F_2 derived from Equation (3). This technique was applicable for all year classes except 1960 and 1961, where no 2-yr-old fish were available in the landing data, the 1976 year class where no 3-yr-old fish were available in the landing data, and the 1972 year class, where the 2-yr-old fish apparently were not fully recruited. For the 1960 and 1961 year classes, trial and error adjustments were made to the starting F value until the annual F_3 estimate for the 1961 year class and the annual F_4 estimate of the 1960 year class were virtually equal to the unweighted mean F_3 estimate derived from the sequential computations of the 1963-71 and 1973-75 year classes. Similarly, the mean F_2 estimate was used for the 1976 year class and the mean F_3 estimate for the 1972 year class.

Estimates of number-at-age by quarter by year class obtained from cohort analysis permitted the reconstruction of population structure for the exploited gulf menhaden stock from 1964 to 1977 (Table 3). Numbers of newly recruited age-1 fish varied as much as threefold between years. Because age-1 fish were numerically the most abundant age group each year, the population size fluctuated in close concert with their numbers (Fig. 3).

Resultant age-specific annual F's by fishing season demonstrate that 1-yr-olds are incompletely recruited to the fishery and that age 2's are fully recruited (Table 4). These results are in accord with those of Ahrenholz (1981), who concluded that fish from more distant eastern and western areas of the Gulf of Mexico (Gulf) shifted toward the more heavily fished central Gulf areas as they aged. The slightly higher values for both the weighted and unweighted mean F's for 3- and 4-yr-olds could be due to either small numbers of fish from the most distant eastern

TABLE 3.—Population size (in millions) of gulf menhaden on 4 April estimated by cohort analysis, 1964-77.

	Age			
Year	1	2	3	4
1964	8,169.2	2,048.0	156.8	5.5
1965	9,796.0	1,329.2	105.0	7.4
1966	5,703.8	1,111.9	41.9	5.2
1967	9,215.6	548.5	14.4	0.0
1968	9,256.7	1,249.0	47.6	0.3
1969	19,311.9	1,539.6	44.6	0.0
1970	12,454.5	3,817.6	59.4	0.0
1971	15,860.1	2,635.0	289.3	4.7
1972	9,580.3	2,704.4	97.0	25.6
1973	15,793.9	1,796.2	181.5	2.6
1974	15,107.1	3,849.3	99.6	0.0
1975	10,220.9	3,324.1	668.4	5.5
1976	11,467.8	2,216.2	435.6	0.0
1977	18,584.2	1,739.4	181.4	57.9

and western areas reaching the more intensively fished waters, or simply a sampling variance. The F estimates from cohort analysis for age-3 and age-4 fish are somewhat suspect, especially for age 4, since the cohort analysis technique used (iterating to a preset F_2) actually makes the F_3 and F_4 estimates of a forward computational nature, rather than backward as for age 1. The divergent nature of the estimates is clearly evident in the values for age 4, although the mean value is realistic for subsequent yield computations, and numbers of fish at this age are of very low magnitude as well.

Because a year class is well represented in the fishery for only 3 yr, a short time span is available for the convergence of estimates of numbers and fishing mortality. This short time span was apparently adequate, however, as cohort runs on the year classes with 4-yr-olds in the landings, using starting estimates of F for age 4 obtained from catch curves, converged to very similar estimates to those obtained by the analysis used here. Ulltang (1977) emphasized that when F is high, convergence is rapid.

FIGURE 3.—Population number of gulf menhaden as of 4 April 1964-77, Estimated from cohort analysis on 1960-76 year classes.

TABLE 4.—Annual instantaneous fishing mortality rate (F) for gulf menhaden for ages 1-3, by year, 1964-77, and fishing mortality rate applied at age 4 (age 3 for year classes without age-4 landings) to initiate the cohort analysis.

	F			
Year	Age 1	Age 2	Age 3	Age 4
1964	0.7182	1.8706	1.9547	1.9504
1965	1.0757	2.3576	1.9112	0.3546
1966	1.2431	3.2468	2.5992	0.1399
1967	0.8991	1.3447	2.7786	0.0000
1968	0.6938	2.2323	1.4032	[1]10.6065
1969	0.5211	2.1553	1.6225	0.0000
1970	0.4521	1.4760	1.4392	0.0000
1971	0.6681	2.2033	1.3287	[1]10.4097
1972	0.5740	1.6024	2.5195	0.2688
1973	0.3120	1.7933	2.0281	1.2313
1974	0.4140	0.6507	1.7885	0.0000
1975	0.4287	0.9322	1.9484	0.1950
1976	0.7860	1.4030	0.9184	0.0000
1977	0.4375	2.1293	1.4229	0.1923
Mean F (unweighted)	0.6588	1.8141	1.8331	1.8106

[1]Initial F set equal to 10.0.

The short-term impact of the fishery on the stock can be assessed by comparing the estimated number-at-age in the population for any given year with the number-at-age landed by the fishery, or simply by using the estimated rate of fishing and calculating the exploitation rate (u) by

$$u_n = (F_n (1 - e^{-(F_n+M)}))/(F_n + M). \qquad (4)$$

From 1964 to 1977 the fishery took an average of 31% of the 1-yr-olds in the population and about 61% of the older fish each year. At these exploitation rates the population loses 52% of the age-1 fish and 35% of the older fish to natural mortality.

The short-term impact on the entire population was determined by 1) calculating a mean F weighted by the number of individuals taken by age for ages 1-3 and then estimating u by Equation (4) and 2) directly comparing numbers landed with the reconstructed population sizes. The average annual loss of individuals from the population to the fishery was about 40% by both methods. However, recruitment is only partial at age 1, and u is much higher at older ages. Natural mortality losses averaged about 47%/year for the overall population. In the absence of fishing, annual losses to natural mortality would be about 67% for all ages.

A measure of how a unit of fishing effort affects the population is commonly quantified through its effect on F. Traditionally this effect, the catchability coefficient (q), is assumed to be a constant. The total fishing effort times this constant should equal F for the year:

$$F = qf \quad (5)$$

where f = a unit of fishing effort (here, a vessel-ton-week).

Estimates of q for the 1964-77 fishing years were obtained by solving for q in the above equation for the population F for ages 1-3 ($\bar{F}_{1\text{-}3}$) weighted by number taken at age, and also for the population total F (Table 5). The resultant q's are quite variable (in excess of fourfold). Estimates of q were plotted against corresponding population size to determine if the catchability coefficients were independent of this variable (Fig. 4). An inverse relationship was noted, a situation which also exists for the Atlantic menhaden (Schaaf 1975b). The data were fitted to the power function to demonstrate the curvilinear inverse relationship.

SPAWNER-RECRUIT RELATIONSHIP

The cohort analysis provides estimates of population size at ages 1-4 from 1964 to 1977. All fish mature by the end of their second year, and spawning apparently reaches a peak in December and January (Lewis and Roithmayr 1981). Therefore, estimates of number-at-age in the population as of 1 January were used to provide estimates of spawning stock size and subsequent recruitment (Table 6). Spawning stock was identified as all fish that had reached at least their second birthday by 1 January. Lewis and Roithmayr also showed that length accounted for a greater porportion of the variance in fecundity than either age or weight. Our fecundity estimates, assuming a 1:1 sex ratio, were based on Lewis and Roithmayr's relationship:

$$\log_e E = -9.8719 + 3.8775 (\log_e l) \quad (6)$$

where E = fecundity in number of eggs and
l = fork length in millimeters.

Because there was little variation in size at age by year class, and the differences noted were not related to population size, estimates of mean length-at-age were obtained from the overall von Bertal-

TABLE 5.—Estimated gulf menhaden population size as of April 4, number caught by year, population exploitation rate (u), estimated population fishing mortality rate (F), population catchability coefficient (q) × 10^{-3}, weighted annual mean fishing mortality rate from cohort analysis ($\bar{F}_{1\text{-}3}$), and the corresponding $\bar{F}_{1\text{-}3}$ catchability coefficient (q) × 10^{-3} calculated from vessel-ton-weeks (Table 1), 1964-77.

Year	Population size (millions) age 1-4	Number caught (millions) age 1-4	Population u	Population F	Population $q \times 10^{-3}$	$\bar{F}_{1\text{-}3}$	$q_{1\text{-}3} \times 10^{-3}$
1964	10,399.5	4,612.8	0.444	1.10	4.03	1.0886	3.99
1965	11,237.6	5,925.8	0.527	1.46	4.35	1.2946	3.86
1966	6,862.8	4,008.0	0.584	1.78	4.67	1.6785	4.40
1967	9,778.5	4,449.6	0.455	1.14	2.82	0.9346	2.31
1968	10,553.6	4,188.7	0.397	0.93	2.46	1.0176	2.64
1969	20,896.1	6,808.3	0.326	0.70	1.70	0.7687	1.87
1970	16,331.5	5,488.0	0.336	0.73	1.83	0.8682	2.17
1971	18,789.1	7,771.3	0.414	0.99	2.09	1.0455	2.21
1972	12,407.3	4,835.0	0.390	0.90	2.01	0.9456	2.11
1973	17,774.2	4,204.6	0.237	0.47	1.10	0.7377	1.73
1974	19,056.0	5,206.5	0.273	0.56	1.15	0.4935	1.02
1975	14,218.9	4,394.4	0.309	0.66	1.23	0.7433	1.38
1976	14,119.6	5,981.0	0.424	1.02	1.77	0.9215	1.60
1977	20,562.9	6,121.4	0.298	0.63	1.18	0.7890	1.48

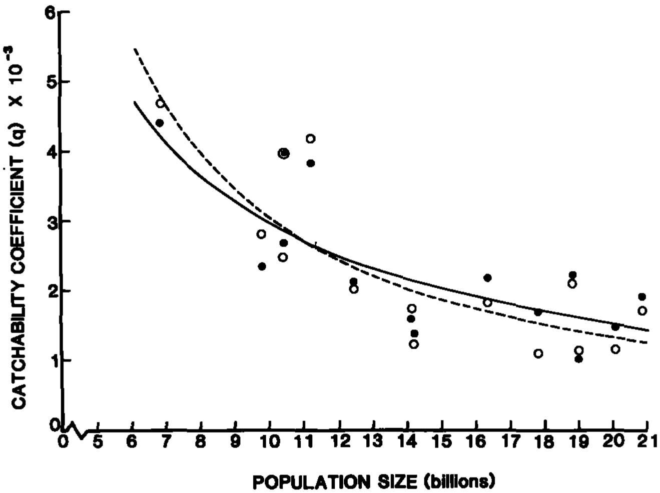

FIGURE 4.—Catchability coefficients calculated from population fishing mortalities (open circles, dashed line), and from cohort annual weighted mean fishing mortalities (dots, solid line) plotted on population number estimated as of 4 April, for the 1964-77 fishing seasons (see Table 5).

TABLE 6.—1 January estimates of number of spawners, number of eggs produced by the spawning stock, biomass of the spawning stock, and number and biomass of recruits at age 1 for gulf menhaden. Preliminary estimates in parentheses.

Year	No. at age (millions) 2	3	4	Total spawners (millions)	No. of eggs (trillions)	Spawning biomass (t)	Resultant recruitment (millions)	Recruitment biomass (t)
1964	2,696.3	206.4	7.2	2,909.9	36.1	305,468	12,896.7	410,630
1965	1,749.9	138.2	9.7	1,897.8	23.7	200,150	7,519.5	239,421
1966	1,463.9	55.1	6.8	1,525.8	18.4	156,705	12,138.2	386,480
1967	722.2	19.0	—	741.2	8.8	75,118	12,186.7	388,025
1968	1,644.3	62.6	0.4	1,707.3	20.5	174,454	25,424.7	809,522
1969	2,026.9	58.7	—	2,085.6	24.8	211,752	16,396.8	522,074
1970	5,026.0	78.2	—	5,104.2	60.0	513,461	20,889.9	665,134
1971	3,472.8	382.4	6.2	3,861.4	49.0	412,808	12,618.5	401,773
1972	3,565.3	127.7	33.7	3,726.7	45.2	384,521	20,796.4	662,157
1973	2,365.8	239.0	3.4	2,608.2	32.8	277,323	19,889.0	633,266
1974	5,067.7	131.1	—	5,198.8	61.7	526,725	13,456.1	428,442
1975	4,376.3	879.9	7.3	5,263.5	70.5	588,668	(15,097.7)	(480,711)
1976	2,917.7	573.5	—	3,491.2	46.6	389,073	(24,466.7)	(779,020)
1977	(2,290.0)	238.8	76.2	(2,605.0)	(34.3)	(286,686)		
1978	(5,258.5)	(90.6)	19.2	(5,368.3)	(63.6)	(543,194)		

anffy growth function presented earlier. Thus, length-at-age estimates are taken as constants, and differences in among year estimates of egg production are due to differences in both total numbers and age composition of the spawning stock (Table 6). Similarly, the weight-length relationship was used in conjunction with the mean length-at-age estimates to obtain weight-at-age estimates for computation of spawning and recruitment biomass (Table 6).

Least-square regressions of second and third degree polynomials were run with numbers of recruits on number of spawners to determine the general shape of the spawner-recruit relationship. Dome-shaped functions provided the least residual sum of squares, indicating that a Ricker-type curve (Ricker 1975) is appropriate. A Ricker-type function has been applied to Atlantic menhaden data (Nelson et al. 1977), and the same criteria appear to apply to gulf menhaden data, i.e., that there is a size-dependent fecundity relationship and that adult menhaden are filter feeders which are known to ingest their own eggs. Additionally, the calculation of an index of density dependence, as detailed by Cushing (1971) ($\log_e$ recruitment regressed on $\log_e$ spawning stock), provides a slope of 0.159. This slope, plus the average fecundity of gulf menhaden (about 25,000 eggs/female) places the gulf menhaden among Cushing's clupeoid groups which have a slightly domed spawner-recruit curve. Accordingly, a spawner-recruite relationship was applied of the form:

$$R = Se^{(S_r - S)/S_M} \quad (7)$$

where R = recruitment at age 1
S = spawning stock size
e = base of natural logarithm
S_r = maximum equilibrium stock
S_M = spawning stock size yielding maximum absolute recruitment.

The model, fitted by a nonlinear least squares technique (Marquardt 1963), predicts an average maximum recruitment of 18.4 billion individuals at a spawning stock of 3.22 billion (Table 7). The curve is a reasonably good fit (Fig. 5), considering the variability inherent in clupeoid recruitment. Data were available over a wide range of spawning stock sizes and recruitment levels. Although recruitment tended to fluctuate widely at lower spawning stock sizes, estimates appear to converge at higher spawning stock levels, indicating the possibility of a strong density-dependent response as spawning stock size increases. The Ricker function appears to describe the data, thus an estimate of spawning stock size premits a general estimate of anticipated recruitment at moderate to high numbers of spawners.

Because fecundity increases with age and because age structure of spawners varies from year to year, estimates of the number of eggs produced should provide a more accurate estimate of spawning stock size than estimates of the numbers of spawners. When the Ricker equation was fitted to number of eggs and number of recruits, the estimate of optimum spawning stock size was similar to the estimate based on the number of spawners and recruits (Table 7) (S_M of 39.66 trillion eggs = 2.3 billion spawners). The unrealistic replacement level (S_r) of 283.32 trillion eggs was generated by scaling factors involved in the comparison of unequal spawner and recruit units (Ricker 1975). Applying the function to spawning and recruitment biomass also provided similar estimates of maximum recruitment and optimum spawning stock size (Table 7,

TABLE 7.—Ricker spawner-recruit estimates of maximum equilibrium stock (S_r), stock size for maximum recruitment (S_m), and recruitment at S_m, for models incorporating number of spawners on number of recruits, number of eggs on number of recruits, and spawning biomass on recruitment biomass, 1964-76 year classes of gulf menhaden.

	Maximum equilibrium stock (S_r)	Stock for maximum recruitment (S_m)	Recruitment at S_m
No. of spawners on no. of recruits	8.83 billion	3.22 billion	18.42 billion
No. of eggs on no. of recruits	283.32 trillion	39.66 trillion	18.48 billion
Spawning biomass on recruit biomass	524,172 t	336,011 t	588,236 t

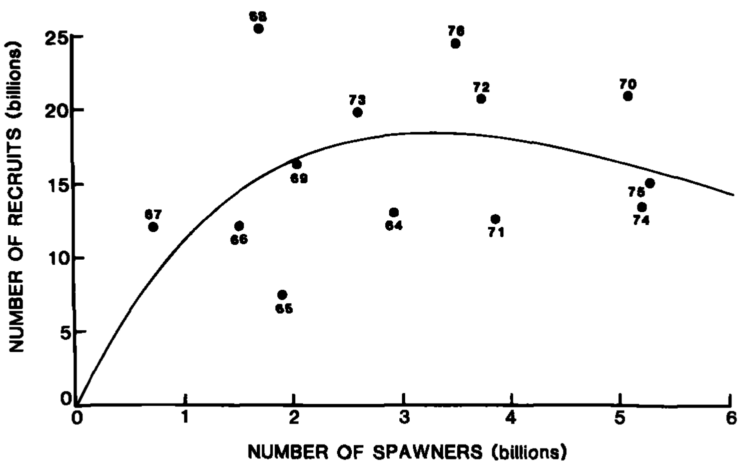

FIGURE 5.—Ricker spawner-recruit relationship for number of spawners and recruits at age 1, estimated as of 1 January, for the 1964-76 gulf menhaden year classes.

Fig. 6). The maximum recruitment level of 588,236 t is equal to about 18.5 billion recruits. The optimum spawning stock biomass of 336,011 t is equal to about 3.2 billion spawners, assuming the age distribution for the spawning stock is average. The function for biomass accounts for changes in age structure of the spawning stock and since age-2 fish consistently represent over 90% of the spawners, differences between plots of numbers and biomass (Figs. 5, 6) are minor.

Spawning stock size has generally remained within a range of potentially good recruitment and has not undergone years of extreme highs or lows (Figs. 5, 6). Trends indicating a steady decrease or increase in stock size and recruitment are not apparent, although the general increased level of recruitment in recent years may be part of a cyclic recruitment fluctuation that is found in many stocks.

YIELD-PER-RECRUIT

We applied what is essentially a Ricker type yield-per-recruit model that was initially developed to evaluate a multiple-gear fishery (M-GEAR) and later modified to accommodate a multiple-area fishery (M-AREA) (Lenarz et al. 1974; Epperly et al. 1979[4]). Yield is summed by time intervals, and individual weights and estimates of natural and fishing mortality can be inserted for each interval (Ricker 1975). An option developed by Epperly et al. (fn. 4) allows for calculation of biomass within intervals by either exponential or arithmetic means. We applied the model in its simpliest form: one set of growth data because the stock was not divided into subareas, constant natural mortality rate, and the exponential growth mode for biomass calculation. The year was divided into quarters to simulate the seasonal nature of the fishery (Table 8). Quarterly fishing mortality rates were developed from the cohort analysis. Estimates were obtained for periods of low population size and high fishing mortality (1964-68), high population size and low fishing mortality (1974-77), and "average" population size and mortality (1964-77) (Table 8). Age of entry into the fishery was

[4]Epperly, S. P., W. H. Lenarz, L. T. Massey, and W. R. Nelson. 1979. A generalized computer program for yield per recruit analysis of a migrating population with area specific growth and mortality rates. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

TABLE 8.—Input array of quarterly length (mm), weight (g), and fishing mortality rates (*F*) used in the calculation of yield-per-recruit of gulf menhaden under average fishing conditions (1964-77), years of low stock size (1964-68), and years of high stock size (1974-77).

Age	Months	$\bar{L}$	$\bar{W}$	$\bar{F}$ (64-77)	$\bar{F}$ (64-68)	$\bar{F}$ (74-77)
0.50	July-Sept.	84.7	10.1	0.0013	0.0018	0.0008
0.75	Oct.-Dec.	103.5	19.5	0.0003	0.0001	0.0005
1.00	Jan.-Mar.	120.2	31.8	0.0002	0.0004	0.0000
1.25	Apr.-June	135.1	46.6	0.1850	0.2677	0.1244
1.50	July-Sept.	148.2	63.2	0.4437	0.6315	0.3593
1.75	Oct.-Dec.	160.0	81.0	0.0299	0.0264	0.0329
2.00	Jan.-Mar.	170.4	99.5	0.0002	0.0000	0.0000
2.25	Apr.-June	179.6	118.2	0.4478	0.5652	0.3683
2.50	July-Sept.	187.8	136.8	1.2213	1.5858	0.8253
2.75	Oct.-Dec.	195.1	154.9	0.1448	0.0594	0.0852
3.00	Jan.-Mar.	201.6	172.3	0.0003	0.0000	0.0000
3.25	Apr.June	207.3	188.9	0.4500	0.5407	0.2966
3.50	July-Sept.	212.4	204.5	1.2722	1.5752	1.0670
3.75	Oct.-Dec.	216.9	219.1	0.1106	0.0133	0.1557
4.00	Jan.-Mar.	221.0	232.7	0.0000	0.0000	0.0000
4.25	Apr.-June	224.5	245.2	0.1605	0.3085	0.0488
4.50	July-Sept.	227.7	256.7	1.6501	2.3018	0.0480
4.75	Oct.-Dec.	230.5	267.2			

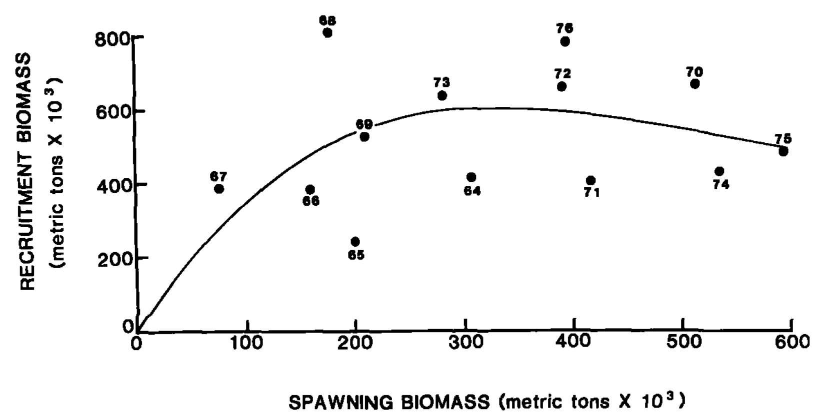

FIGURE 6.—Ricker spawner-recruit relationship for biomass of spawners and recruits at age 1, estimated as of 1 January, for the 1964-76 gulf menhaden year classes.

0.5 yr of age, the age at which gulf menhaden first appear in the catch in extremely small numbers and have a very low fishing mortality rate. Fishing mortality occurs principally during the 2d and 3d quarters of the year (April-September) (Table 8). Various multiples of the average fishing mortality at each age were used to simulate effects of increased or decreased fishing mortality (Table 9).

landings in the fishery of 487,736 t by only 2.6% for 1964-77.

Yield-per-recruit for the years of higher and lower levels of fishing mortality (Table 8) was estimated to be 18.20 and 15.78 g under F-multiples of 1.00 and age of entry at 0.5. Trends were identical to those for average 1964-77 conditions, and thus are not presented in further detail.

TABLE 9.—Estimates of gulf menhaden yield-per-recruit (g) under average conditions of growth and as multiples of average fishing mortality rate (F-multiple = 1.00), 1964-77, at varying age of entry.

Age at	Multiplier of fishing mortality									
entry	0.25	0.33	0.50	0.66	0.75	1.00	1.25	1.50	1.75	2.00
4.50	0.96	1.19	1.60	1.90	2.04	2.34	2.54	2.69	2.79	2.86
4.25	1.06	1.31	1.75	2.07	2.21	2.52	2.73	2.87	2.98	3.05
4.00	1.06	1.31	1.75	2.07	2.21	2.52	2.73	2.87	2.98	3.05
3.75	1.18	1.46	1.96	2.31	2.48	2.84	3.09	3.28	3.43	3.55
3.50	2.73	3.32	4.28	4.93	5.21	5.80	6.20	6.47	6.67	6.81
3.25	3.32	4.01	5.10	5.81	6.12	6.74	7.15	7.43	7.63	7.78
3.00	3.32	4.01	5.10	5.81	6.12	6.74	7.15	7.43	7.63	7.79
2.75	3.63	4.38	5.58	6.38	6.73	7.45	7.96	8.33	8.62	8.86
2.50	6.39	7.62	9.51	10.71	11.23	12.27	12.95	13.41	13.74	13.98
2.25	7.43	8.80	10.86	12.12	12.66	13.71	14.37	14.82	15.14	15.37
2.00	7.43	8.80	10.86	12.12	12.66	13.71	14.37	14.82	15.14	15.37
1.75	7.52	8.91	10.99	12.27	12.82	13.89	14.57	15.04	15.38	15.63
1.50	8.91	10.52	12.93	14.43	15.07	16.36	17.22	17.83	18.30	18.67
1.25	9.45	11.13	13.62	15.15	15.80	17.09	17.94	18.53	18.97	19.30
1.00	9.45	11.13	13.62	15.15	15.80	17.09	17.94	18.53	18.97	19.30
0.75	9.45	11.13	13.62	15.16	15.80	17.09	17.94	18.53	18.97	19.30
0.50	9.45	11.13	13.62	15.15	15.80	17.09	17.93	18.52	18.95	19.28

The yield-per-recruit increases only slightly with a delayed age-of-entry and then drops rapidly because of the high rate of natural mortality. The model predicts maximum cohort biomass at an age of 1.5, before gulf menhaden are fully recruited into the fishery. The high natural mortality rate requires that substantial fishing mortality be applied at a young age if gulf menhaden are to be harvested near their peak biomass.

A three-dimensional representation of yield-per-recruit (Table 9) is helpful in depicting the seasonal nature of the fishery (Fig. 7). Since most of the fishing mortality on age-1, -2, and -3 fish is applied during the 2d and 3d quarters (ages of X.25 and X.50), the impact of delaying recruitment past those quarters results in a sharp decline in yield-per-recruit, due to the high rate of natural mortality.

Predicted catches based on yield-per-recruit were compared with actual catch during 1964-77. Average recruitment at age 1 (16,030 billion), estimated from the cohort analysis, was back calculated to age 0.5, the age of initial entry, and multiplied by the 17.09 g/recruit predicted by the model. The resultant estimate of 474,829 t differs from the average

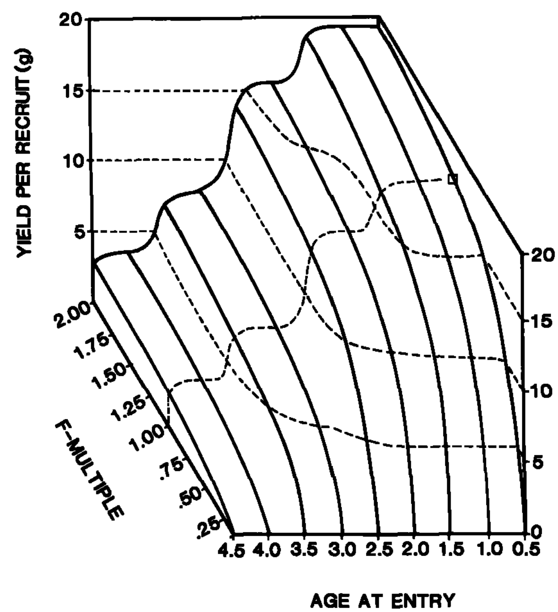

FIGURE 7.—Yield-per-recruit of gulf menhaden under average conditions of growth and with multiples of average fishing mortality by 3-mo interval (F-multiple = 1.0) for the 1964-77 fishing seasons (average conditions indicated by □).

SUSTAINABLE YIELD AND POPULATION SIMULATION

Production functions were developed from the 1946-79 catch and effort data to provide an estimate of maximum sustainable yield (MSY) for gulf menhaden. Application of a standard parabolic surplus production model (Schaefer 1954, 1957) yields an MSY estimate of 553,000 t at 555,000 vessel-ton-weeks. Past updates of MSY for the Gulf fishery have shown continual increases as additional years are added. Chapoton (1972) estimated an MSY of 430,000 t for the 1946-70 period, and Schaaf's (1975a) estimate of 478,000 t included the 1971 and 1972 catch and effort.

For the years in which estimates of catchability coefficient (q) were calculated (1964-77) nominal effort was adjusted to the mean population q of that period. For that time period, mean catchability coefficient was divided by the estimate of population F each year, to provide an estimate of effort adjusted for "average" conditions from 1964 to 1977.

A parabolic surplus production function was applied to the 1946-79 data set, with adjusted effort used instead of nominal effort for 1964-77. The results were similar to model results using nominal effort with an estimated MSY of 541,904 t at an effort of 505,483 vessel-ton-weeks (Fig. 8). A generalized stock production model (PRODFIT) which allows the shape of the curve to vary based on a least squares fit to the data (Fox 1975) was also applied, yielding an estimate of MSY of 636,886 t at an effort of 531,201 vessel-ton-weeks (Fig. 8).

The two curves provide estimates that vary by about 95,000 t with the PRODFIT model indicating a sharp drop in yield after MSY is exceeded.

An estimate of MSY based on biological characteristics should be more reliable than one based on yield and nominal effort, particularly when there is not a clear nominal effort-effective effort relationship. Accordingly, we applied a population simulation model (Walters 1969) for the 1964-77 period which incorporated our estimates of growth, spawner-recruit relationship, fishing mortality, and natural mortality. This estimated the impact of fishing mortality on stock and yield at an array of fishing mortality rates. The model can also iterate to MSY. Underlying assumptions of the Walters' model are that the 1) spawner-recruit relationship incorporated is realistic, 2) array of F's accurately reflect the distribution of fishing effort and availability at age, and 3) time increment estimates of weight are sufficiently brief to realistically estimate both population and catch biomass during the fishing periods. The model calculates population biomass, yield, residual spawners of age 2 and greater, and incoming recruitment. We used weight-at-age data described in the section on average size and growth (Equations (1) and (2)), and used the spawner-recruit relationship developed for the number of spawners and recruits (Equation (7)). The instantaneous natural mortality rate was 1.1 as discussed earlier. Fishing mortality could not precisely mimic that for the fishery, because the program requires either zero fishing mortality or a constant fishing mortality for any within-year increment. However, it does allow for an array of multipliers at a given fishing mortality, providing different F's for each age, if desired. Therefore, we were able to vary fishing mortality by age, but used either zero or a constant fishing mortality for quarterly increments within each year. Since fishing mortality was essentially zero on age-0 fish and was inconsistent between years, a fishing mortality rate of zero was applied to that age group. For age groups 1-4, all of the fishing mortality was by definition imposed equally in quarters 2 and 3 (April-June, July-September), and no fishing mortality was applied in quarters 1 and 4, even though we knew that fishing mortality during the July-September period was consistently higher than that observed for the

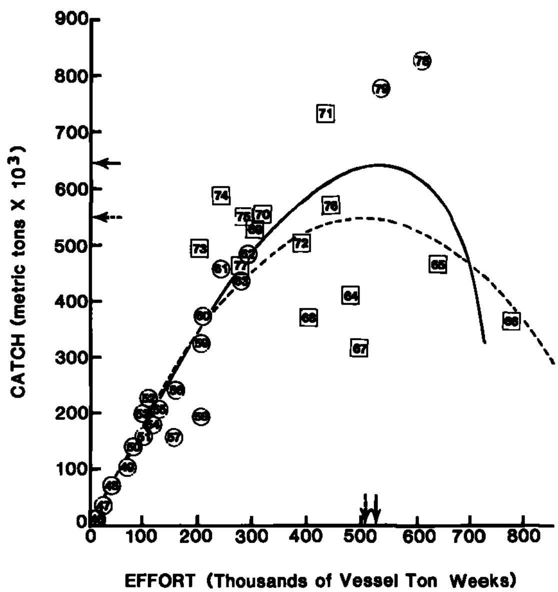

FIGURE 8.—Parabolic (dashed line) and prodfit (solid line) surplus production function models fitted to catch and effort data for the gulf menhaden fishery from 1946 to 1979, with 1964-77 data being estimates of effective effort, based on adjustments from calculated catchability coefficients for those years.

previous quarter (i.e., the same nominal effort was applied to a smaller population). The result was that yield was overestimated for April-June and underestimated for July-September, but estimated reasonably accurately for the season.

We attempted to simulate reality by using multiples of the fishing mortality distribution that we observed in the 1964-77 data base. Fishing mortality imposed to mimic current conditions was obtained by taking the mean fishing mortality at age by quarter from the cohort analysis conducted on the 1960-76 year classes (1964-77 fishing years). The mean mortality on ages 2-4 fish was used, along with a mortality obtained from a scaling factor of 0.362 for age 1 (Table 10). Input population size to start the simulation runs was the mean population number-at-age as of 1 January, the arbitrarily assigned birth date of gulf menhaden. Those numbers were 16,030 million, 2,813 million, 227.9 million, and 10.78 million for ages 1-4. The model was run over a range from 0 to 2.75 times the average fishing mortality and was also used to iterate to MSY under the current distribution of fishing mortality by age (Table 10).

The overall catch-effort curve from multiple runs indicates that the fishery is operating slightly before the MSY level (Fig. 9, Table 10). At the current *F*-multiple of 1.0, the fishery should sustain an average yield of about 565,581 t, assuming no variance in recruitment from the hypothetical spawner-recruit curve.

The model predicts a MSY of about 585,118 t at 127% of the average fishing mortality for the 1964-77 fishing seasons. We feel that this model, which incorporates a spawner-recruit relationship and recruitment pattern plus growth and natural mortality rates, provides a better estimate of long-term MSY than does a model based on a simple catch-effort production function. Considerable fluctuation in yield will result from fluctuations in recruitment, but the long-term MSY estimate appears to be realistic, provided that the estimated spawner-recruit relationship is valid and that the basic pattern of recruitment remains unchanged.

The Walters' model also identifies the level of fishing mortality at which the population is no longer sustainable, i.e., a biological break-even point. The extinction point occurs at an *F*-multiple of 2.50 (150% greater than current fishing mortality), although the model indicates that such extinction would involve a gradual decline over a period of many years, again assuming that "average" conditions prevailed (Fig. 9). Increasing the fishing mortality beyond an *F*-multiple of 2.50 results in a more rapid rate of extinction (Table 10).

Results of low and high *F*-multiple levels show steep slopes on the ascending and descending limbs of the production function curve (Fig. 9). The ascending limb behaves similarly to the curves in the yield-per-recruit model as fishing mortality rates go from low to current levels (Fig. 7). At mortality rates higher than current levels, however, the yield-per-recruit model cannot be used to evaluate potential yield because of the impact of heavy fishing mortality on the spawning stock and the subsequent reduction in recruitment. For example, under the average recruitment level of 16.03 billion fish at age

TABLE 10.—Annual age-specific fishing mortality rates for gulf menhaden, expressed as multiples of the average fishing mortality rate at age, 1964-77, (*F*-multiple = 1.00), actual fishing mortality rates at age used in the population simulation model, sustainable yield, population biomass, and years to stabilization.

F-multiple	Actual *F* at age 0	Actual *F* at age 1	Actual *F* at age 2-4	Sustainable yield level (t)	Population biomass (t)	Years to stabilization
0	0	0	0	0	1,268,348	97
0.25	0	0.1647	0.4550	266,878	1,151,345	53
0.50	0	0.3294	0.9100	419,813	1,072,885	35
0.75	0	0.4941	1.3650	512,568	1,009,288	27
1.00	0	0.6588	1.8200	565,581	945,740	8
1.25	0	0.8236	2.2750	585,010	871,695	20
1.27 (MSY)	0	0.8367	2.3114	585,118	865,300	22
1.50	0	0.9883	2.7300	569,823	778,012	32
1.75	0	1.1530	3.1850	514,388	655,278	42
2.00	0	1.3177	3.6400	409,304	492,702	78
2.25	0	1.4824	4.0950	241,462	277,288	210
2.50	0	1.6471	4.5500	0	0	[1]>300
2.75	0	1.8118	5.0050	0	0	[1]250

[1]To extinction.

1 (28.34 billion at age 0.5) and an *F*-multiple of 2.00, the yield-per-recruit model predicts a total yield of 546,395 t; the population simulation model predicts a gradual decline from current levels and stabilization at about 409,304 t. Thus, when using average recruitment levels and yield-per-recruit results, estimates of yield at *F*-multiple levels higher than about 1.75 times the average fishing mortality for the 1964-77 period will be unrealistic.

The impact of increasing levels of fishing mortality on the stock is also reflected in estimates of population biomass under an array of *F*-multiples (Table 10). Biomass estimates were based on predicted population size as of 1 January (i.e., after recruitment and before application of fishing mortality). These estimates show a pre-exploitation population biomass exceeding 1.268 million t, followed by an accelerating decline as increased fishing mortality takes progressively larger fractions of the population and disproportionately larger fractions of older and heavier fish.

STATUS AND OUTLOOK FOR THE GULF MENHADEN FISHERY

The gulf menhaden population appears to be healthy, highly productive, and capable of supporting yearly harvests exceeding 500,000 t, although considerable variation can be expected. It has shown a general increase in abundance through the period covered in this report, although this increase may be a portion of a general cycle of this clupeid stock.

The high natural mortality rate indicates that fishing mortality has to be applied at a fairly high rate and on young fish to avoid loss of surplus biomass. Peak cohort biomass is reached at an age of 1.5 yr. It is not all available to the fishery, because age-1 fish are only partially recruited. Partial recruitment appears to have some benefit in that it affords some protection for the spawning stock.

Recruitment fluctuation appears to be greater at low spawning stock sizes. Initial spawning before full recruitment would assure moderate to high levels of recruitment and reduce chances for large recruitment fluctuation. Therefore, if recruitment failure were to occur, it would likely arise from biotic or environmental factors rather than from excessive fishing mortality.

Significant increases in fishing mortality are unlikely to occur, given the present distribution and operating procedure of the fishery, unless there is a series of recruitment failures. The current fleet of about 80 purse seine vessels appears to be more than adequate to harvest the recruited gulf menhaden stock during years of low to moderate stock size, and

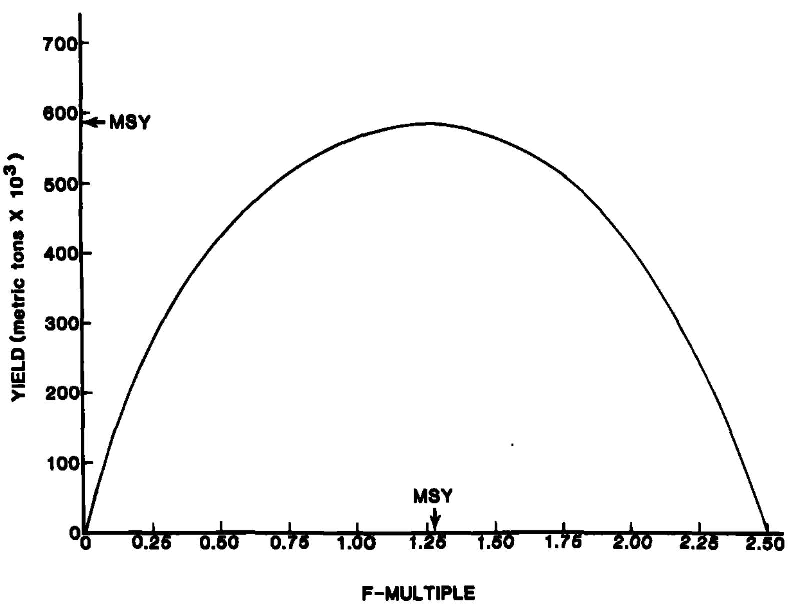

FIGURE 9.—Sustainable yield predicted by a deterministic population simulation model of the gulf menhaden fishery at multiples of the average fishing mortality (F-multiple = 1.00) for the 1964-77 fishing season (see Table 10 for scaling values).

capable of taking advantage of those years when a large harvestable stock is available (1971, 1978, and 1979). Total mortality rates (averaging 83% for age-1 fish and 95% for ages 2-4 fish) are extremely high. Major expansions of the fleet and processing facilities necessary to substantially increase the fishery's share of population biomass would require enormous capital investment. Based on results of the simulation model, large increases in fishing effort would also result in an overall average decline in landings that would likely be followed by an economically forced reduction in effort. Under present circumstances, we do not envision the sustained intensification of effort necessary to drive the gulf menhaden stock to biological extinction.

The simulation model estimates that the effort currently applied in the fishery is probably very close to that which is necessary to produce MSY (Fig. 9), while it exceeds the necessary level in the catch-effort production function (Fig. 8). Assuming that the simulation model reasonably approximates average conditions, some increase in overall yield could be obtained through a modest increase in effort, which has in fact occurred in more recent years.

Based on recruitment levels for 1964-77, it is evident that considerable variation will occur around a long-term sustainable yield level, regardless of the level of fishing mortality. We varied recruitment level in the population simulation model through periods of high (25 billion) and low (10 billion) levels of recruitment to provide estimates of the yield from the fishery under good and poor recruitment regimes, and to observe the rate of response to recruitment changes. The results range from an approximate high of 757,000 t to a low of 303,000 t at the high and low recruitment levels (Fig. 10). Since only age-1 and age-2 fish predominate in the fishery, only 2 years were required for the full impact of a change in recruitment to be shown, with a majority of the impact occurring in the first year. We then allowed the average spawner-recruit relationship to operate, stabilizing yield at 565,580 t. Actual low yield predictions are probably underestimated, in that fishing mortality increases in years of low stock size, and the fishery would produce higher yield than through the fishing mortality imposed under average conditions. Nevertheless, these extremes are near the actual ranges in yield observed in the fishery during the study period (316,100-820,000 t) and should provide reasonable estimates of mean yield and range expected in future years.

Since considerable variation does exist around the spawner-recruit curve and simulations were all conducted in deterministic fashion, the model was run with recruitment varying randomly between the recruitment extremes calculated from our data set (7.5 billion-25.0 billion). The results of that simulation (Fig. 10) provide a long-term (50 yr) average of 467,459 t, but it varies from 718,000 to 263,000 t. We anticipate that the fishery will continue to operate somewhat in this fashion, unless there is a cyclic environmental or biological influence on recruitment.

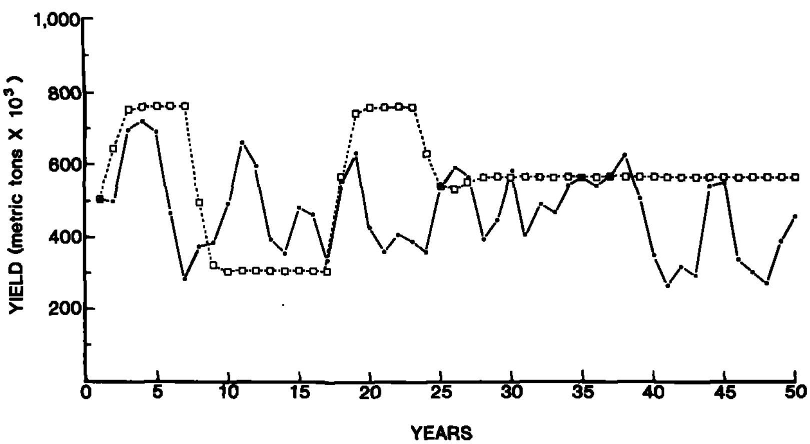

FIGURE 10.—Annual yield of the gulf menhaden fishery projected by the population simulation model when upper and lower values of recruitment from the 1964-77 year classes are inserted (dashed line) and when recruitment varies randomly within limits of observed recruitment for the same data set (solid line).

SUMMARY

The fishery for gulf menhaden appears to be at parity with the stock. There is ample capacity to harvest available biomass and segments of the stock are not available to the fishery until after spawning has occurred. The fishery appears to be near the level of estimated maximum sustainable yield, but will be subject to wide ranges in annual yield. Substantially increased effort will likely reduce long-term average yield, but should not drive the stock to biological extinction. Maintenance of current catch and stock conditions is dependent on the biology of gulf menhaden, the pattern of recruitment, and on maintaining the current fishing strategy. Major changes in the operation of the fishery, such as an expansion of effort east and west of the present range, or offshore on winter spawning concentrations, will change the basis on which these analyses were formulated, and would have consequences which are not predictable at this time.

LITERATURE CITED

ABRAMSON, N. J.
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101, 154 p.

AHRENHOLZ, D. W.
1981. Recruitment and exploitation of Gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 79:325-335.

CHAPOTON, R. B.
1972. The future of the Gulf menhaden, the United States' largest fishery. Proc. Gulf Caribb. Fish. Inst. 24:134-143.

CHRISTMAS, J. Y., JR., AND D. J. ETZOLD.
1977. The menhaden fishery of the Gulf of Mexico United States: a regional management plan. Gulf Coast Res. Lab. Tech. Rep. Ser. 1, 53 p.

CLARK, C. W., AND M. MANGEL.
1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. Fish. Bull., U.S. 77:317-337.

CUSHING, D. H.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Int. Explor. Mer 33:340-362.

FOX, W. W., JR.
1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull., U.S. 73:23-37.

HUNTSMAN, G. R., AND R. B. CHAPOTON.
1973. Biostatistical data acquisition in the menhaden fisheries. Trans. Am. Fish. Soc. 102:452-456.

LENARZ, W. H., W. W. FOX, JR., G. T. SAKAGAWA, AND B. J. ROTHCHILD.
1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares*. Fish. Bull., U.S. 72:37-61.

LEWIS, R. M., AND C. M. ROITHMAYR.
1981. Spawning and sexual maturity of Gulf menhaden *Brevoortia patronus*. Fish. Bull., U.S. 78:947-951.

MARQUARDT, D. W.
1963. An algorithm for least-squares estimation of nonlinear parameters. SIAM J. App. Math. 11:431-441.

MURPHY, G. I.
1965. A solution of the catch equation. J. Fish. Res. Board Can. 22:191-202.

NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF.
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75:23-41.

NICHOLSON, W. R.
1978. Gulf menhaden, *Brevoortia patronus*, purse seine fishery: catch, fishing activity, and age and size composition, 1964-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 722, 8 p.

NICHOLSON, W. R., AND W. E. SCHAAF.
1978. Aging of Gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 315-322.

REINTJES, J. W.
1964. Annotated bibliography on biology of menhadens and menhadenlike fishes of the world. U.S. Fish. Wildl. Serv., Fish. Bull. 63:531-549.

REINTJES, J. W., AND P. M. KENEY.
1975. Annotated bibliography on the biology of the menhadens, genus *Brevoortia*, 1963-1973. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 687, 92 p.

REINTJES, J W., J. Y. CHRISTMAS, JR., AND R. A. COLLINS.
1960. Annotated bibliography on biology of American menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 60:297-322.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

SCHAAF, W. E.
1975a. Status of the Gulf and Atlantic menhaden fisheries and implications for resource management. Mar. Fish. Rev. 37(9):1-9.
1975b. Fish population models: potential and actual links to ecological models. *In* C. S. Russell (editor), Ecological modeling in a resource management framework, p. 211-239. Resources for the Future, Washington, D.C.

SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1:27-56.
1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 2:247-268.

TOMLINSON, P. K.
1970. A generalization of the Murphy catch equation. J. Fish. Res. Board Can. 27:821-825.

ULLTANG, Ø.
1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. Int. Explor. Mer 37:249-260.

WALTERS, C. J.
1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98:505-512.