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Stock Assessment of the Atlantic Menhaden, *Brevoortia tyrannus*, Fishery

Douglas S. Vaughan
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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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ABSTRACT

A stock assessment of the Atlantic menhaden, *Brevoortia tyrannus*, fishery was conducted with purse-seine landings data from 1940 to 1984 and port sampling data from 1955 to 1984. These data were analyzed to determine growth rates, maximum sustainable yield (MSY), spawner-recruit relationships, and yield per recruit. Virtual population analysis was used to estimate stock size, year class size, and fishing mortality rates.

Surplus production models produced estimates of MSY from 450 to 490 kmt compared with yields of 416 to 436 kmt based roughly on maximum recruitment from a weak spawner-recruit relationship. Recruitment to age-1 ranged from 1.2 to 14.8 billion fish for year classes 1955-81. Recent mean recruitment to age-1 for the 1975-81 year classes averaged 5.7 billion fish and compared favorably with the mean of 7.7 billion age-1 fish recruited during the late 1950's. Mean recruitment from recent years suggests possible coastwide yields of 416 to 481 kmt. Continued dominance of late age-2 spawners among the spawning stock is of concern, since the stock is at greater risk through poor recruitment if recent favorable environmental conditions change.

Yield-per-recruit estimates ranged from 46 g to 59 g since 1970. The high dependency of the modern fishery on prespawners has increased concerns about fluctuations in year-to-year availability and catches. To increase yield and enhance the stability of the resource, the number of age classes contributing significantly to the fishery should be increased, creating a buffer against future poor recruitment years and lessening the year-to-year fluctuations in landings.

Introduction

The Atlantic menhaden, *Brevoortia tyrannus*, is a euryhaline species found in coastal and inland tidal waters from Nova Scotia, Canada, to West Palm Beach, Florida (Fig. 1) (Reintjes 1969). They form surface schools off Florida, Georgia, and the Carolinas in April and May as the waters warm, and move slowly northward, stratifying by age and size during the summer (older and larger fish are generally found farther north). A southern migration begins in early fall, with surface schools disappearing in late December or early January off the Carolinas. Spawning occurs principally at sea and in larger bays and sounds from May to October in the North and Middle Atlantic areas and from October to April in the Chesapeake Bay and South Atlantic areas. Eggs hatch at sea and the larvae are moved to estuaries by ocean currents (Nelson et al. 1977) where they metamorphose and develop into juveniles. In late fall and early winter, the juveniles leave the estuaries and move into large bays or the open sea. Adult Atlantic menhaden are filter feeders (feeding primarily on phytoplankton) and, in turn, support predatory food fishes.

A commercial fishery for Atlantic menhaden has existed since colonial times, but purse seines, now the principal gear, were introduced by 1845 (Frye 1978). Large carrier vessels are equipped with a pair of purse boats for setting the seines around the schools of fish. In 1984, eight active reduction plants at five ports on the Atlantic coast (Fig. 1) produced fish meal and solubles used in poultry and livestock feeds, and oil used in paints and as an edible oil in Europe. Landings increased rapidly through the 1940's and early 1950's as fishing effort (measured in vessel weeks) increased (Fig. 2). After several years of high landings and fishing effort in the late 1950's, a sharp decline was observed in landings in the early and mid-1960's. Fishing effort similarly declined during the 1960's. Landings have recovered somewhat since the late 1960's, and represent 38% by weight of the U.S. Atlantic coast commercial fish landings in 1984 (U.S. National Marine Fisheries Service 1985).

The menhaden research program of the National Marine Fisheries Service has maintained records of daily vessel landings and fishing activity since 1955, supplemented in recent years by information from captains' daily fishing reports. Samples of catches for weight, length, and age composition have been used in conjunction with vessel landings to estimate number of fish landed at each age by plant and area, to determine growth rates, and to estimate fishing mortality (Chester 1984). Additional information has also been obtained on fecundity (Higham and Nicholson 1964; Dietrich 1979) and on selected environmental variables (Nelson et al. 1977). Juveniles have been tagged each fall to study movements and to estimate natural mortality (Kroger and Guthrie 1973). An overview of the life history and stock structure of the Atlantic menhaden is presented in Ahrenholz et al. (1987).

The major purpose for this report is to update the analyses presented in Ahrenholz et al. (1987) with three additional years of data (1982-84 fishing years). These analyses include (1) application of virtual population analysis to obtain estimates of population sizes and fishing mortality; (2) analyses of growth to confirm an inverse relationship with population size and use in population models; (3) development of surplus production models to estimate maximum sustainable yield (MSY); (4) development of spawner-recruit models to determine adequacy of recent recruitment and spawning stock; and (5) application of yield-per-recruit approach to determine if greater yields are available given recent levels of recruitment.

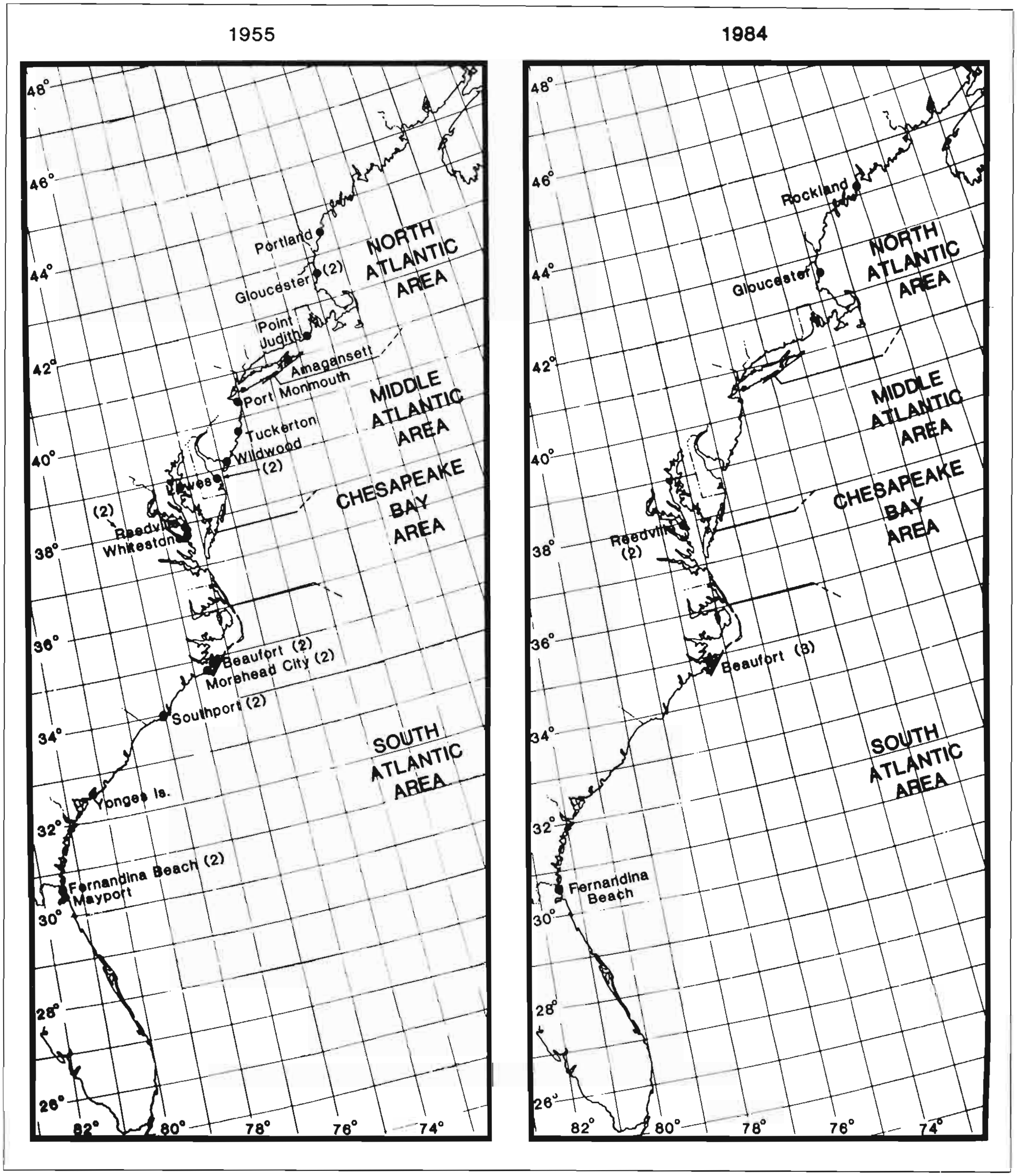

Figure 1

Geographic fishing areas for the Atlantic menhaden purse-seine fishery, and landing ports for 1955 and 1984 fishing years. The number of plants operating at each port is given in parentheses when greater than one.

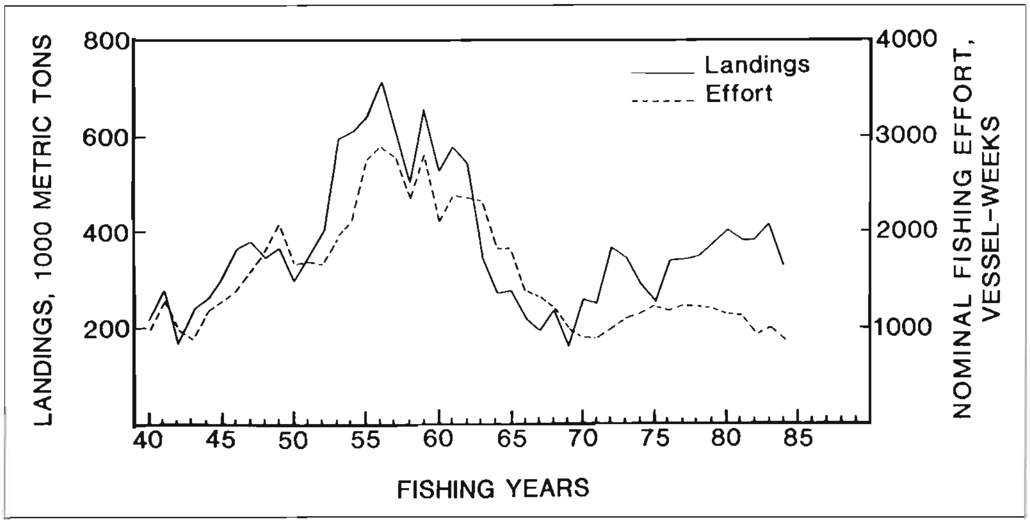

Figure 2
Catch of Atlantic menhaden in thousands of metric tons and fishing effort in vessel weeks for fishing years 1940-84.

Description of the fishery

For purposes of summarization and analysis, June and Reintjes (1959) divided the Atlantic coast into four geographic fishing areas and one temporal fishing area (Fig. 1). With only a change in the boundary line between the South Atlantic and Chesapeake Bay areas (Nicholson 1975), the divisions are:

North Atlantic Area (Area 1) Waters along the southern coast of Long Island, east of a line due south of Moriches Inlet (lat. 40° 46′ N. and long. 72° 44′ W.), and waters northward.

Middle Atlantic Area (Area 2) Waters west of a line running due south of Moriches Inlet, on the southern coast of Long Island, southward to Great Machipongo Inlet, VA (lat. 37° 22′ N. and long. 75° 43′ W.).

Chesapeake Bay Area (Area 3) Chesapeake Bay proper and coastal waters south of Great Machipongo Inlet, VA, to lat. 35° 20′ N. on the North Carolina coast.

South Atlantic Area (Area 4) Coastal waters south of lat. 35° 20′ N. on the North Carolina coast to Cape Canaveral, FL.

North Carolina Fall Fishery (Area 5) A temporal fishing area consisting of waters from Cape Hatteras, NC, south to the southern border of North Carolina, beginning sometime between the last week of October and the second week of November, depending on the arrival of migratory menhaden from more northerly waters, to the end of February of the next calendar year (fishing usually stops by mid-January). For standardized data summary, the week of each season which ends between Nov. 8 and Nov. 14 is taken to be the first week of the fall fishery.

Twenty-three plants operated at 16 ports along the U.S. Atlantic coast from Maine to Florida during 1955, while only eight plants operated at five ports during 1984 (Fig. 1). The number of vessels landing fish declined from 150 during the 1955 fishing season to a low of 38 during the 1984 fishing season (Table 1). Much of this

Table 1
Number of purse-seine vessels that landed Atlantic menhaden during each fishing year by area, 1955-84.

Year	North Atlantic[a]	Middle Atlantic	Chesapeake Bay[b]	South Atlantic[c]	Total[d]	Fall fishery
1955	39	48	20	34	150	51
1956	40	47	24	30	149	63
1957	33	46	25	31	144	64
1958	23	44	28	26	130	63
1959	34	45	31	25	144	59
1960	19	47	22	20	115	37
1961	21	47	23	20	117	44
1962	20	47	29	15	112	49
1963	10	46	36	16	112	46
1964	9	37	38	16	111	51
1965	6	13	38	19	84	46
1966	5	10	36	16	76	43
1967	0	4	32	16	64	46
1968	2	4	25	16	59	45
1969	3	4	22	16	51	36
1970	4	1	18	11	54	37
1971	5	2	20	11	51	32
1972	9	4	19	11	51	5
1973	10	6	23	11	58	4
1974	12	6	22	12	63	12
1975	9	5	22	14	61	17
1976	12	4	21	12	62	13
1977	12	5	24	10	64	16
1978	13	5	22	11	53	18
1979	11	4	22	13	54	18
1980	5	6	24	12	51	19
1981	8	7	23	13	57	19
1982	9	0	22	8	47	18
1983	7	0	24	10	41	17
1984	6	0	26	6	38	12

[a]Vessels fishing from New England ports in recent years are all trawlers that convert to purse seine in summer, some fish regularly and others sporadically.
[b]Vessels that fished only in regular season. Does not include vessels added in October and November.
[c]Includes only vessels that landed regularly in the summer fishery.
[d]Includes all vessels that landed fish during the year.

decline has occurred in the North and Middle Atlantic areas. For example, during 1955 there were 77 vessels operating out of the North and Middle Atlantic areas and 54 vessels out of the Chesapeake Bay and South Atlantic areas compared with only 6 and 32 vessels, respectively, during 1984. During the 1984 fishing year, two small plants operated in the North Atlantic area, none operated in the Middle Atlantic area, two large plants operated in the Chesapeake Bay area, and three small plants operated in the South Atlantic area during the summer season. Two small plants and one large plant operated in Beaufort, North Carolina, during the 1984 North Carolina fall fishery. However, modernization and increased vessel size, coupled with technological innovations to the fishing operations themselves, have substantially increased the potential fishing power of individual vessels (Reintjes 1969; Nicholson 1971).

Table 2
Quarterly time increments used in stock assessment analysis of Atlantic menhaden.

Quarter	Beginning week ending date	Ending week ending date
1	> 2/29	< 6/01
2	> 5/30	< 8/30
3	> 8/29	< 11/29
4	> 11/28	< 2/29[a]

[a]February of next calendar year, but same season.

Virtual population analyses

Estimates of population sizes and fishing mortality rates by age are obtained from virtual population analyses (VPA) as developed by Murphy (1965) and modified by Tomlinson (1970). Tomlinson's computer program MURPHY (Abramson 1971) was used for these calculations which are obtained independently of catch-per-unit-effort (CPUE). Backward sequential computations (oldest age to youngest age) were used because they tend to converge on the same (i.e., true) estimates, while forward calculations tend to diverge unless the true starting value was used.

A major component of the input data for these analyses is catch in numbers-at-age. These data are summarized annually (1955-64) and quarterly (1965-84) (Smith et al. 1987) from daily estimates by sampling methods outlined in Nicholson (1978a). The fishing year is divided into four approximately equal periods beginning March 1 (Table 2). The annual instantaneous natural mortality rate (M) was obtained from Ahrenholz et al. (1987). This estimate (0.45 per year or 0.1125 per quarter) was assumed constant for all ages (greater than 0.5) and years. In the historical data set (1955-84) Atlantic menhaden greater than age-8 were pooled with age-8 fish (Smith et al. 1987).

Three sets of VPA's were conducted on the Atlantic menhaden catch-at-age data. First, a set of annual VPA's was conducted on all year classes from 1947 through 1981. These provided estimates of annual instantaneous fishing mortality rate by age and population size of each age class at the start of each fishing year (March 1). Second, a set of "partial-quarterly" VPA's was conducted on all year classes from 1947 through 1964 based on the assumptions outlined in Ahrenholz et al. (1987). These VPA's, which are actually annual VPA's offset by one quarter, are used to estimate population size-at-age at the start of the fourth quarter (December 1), prior to the onset of the major spawning period from December through February. Finally, a set of quarterly VPA's could be conducted only on year classes from 1965 through 1984. Estimates of instantaneous fishing mortality rates and population sizes are obtained for each age at the start of each quarter.

Results from these VPA's differed slightly from those of Ahrenholz et al. (1987) for two reasons. First, the port sampling data for size and age (1970-84) were examined for errors using recently developed editing programs. Corrections were made to the data set where appropriate based on an examination of the original records. Second, a new method was used to estimate the terminal F used as the starting value in the VPA procedure (Table 3). This estimation

Table 3
Minimimum variance unbiased estimates (MVUE) of terminal F for use in annual virtual population analyis (VPA) of Atlantic menhaden, source of estimate, and ages involved by year class.

Year class	Terminal F	VPA Ages	MVUE Ages[a]
1947	0.4862[b]	8	–
1948	1.3134[b]	7-8	–
1949	0.6673	6-8	6-8
1950	0.5993	5-8	5-8
1951	0.6607	4-8	4-8
1952	0.6821	3-8	3-8
1953	0.8273	2-8	2-8
1954	1.3446	1-8	2-8
1955	1.5300	0-8	2-8
1956	0.8683	0-8	2-8
1957	1.1333	0-8	2-8
1958	1.6425	0-8	4-8
1959	0.7456	0-7	2-7
1960	1.4883	0-6	2-6
1961	1.6770	0-6	2-6
1962	1.7335	0-6	2-6
1963	1.9690	0-6	2-6
1964	1.3676	0-5	2-5
1965	2.1564	0-5	3-5
1966	1.8880	0-5	2-5
1967	1.2648	0-5	2-5
1968	1.2656	0-5	2-5
1969	2.5027	0-6	3-6
1970	2.1135	0-5	2-5
1971	2.5530	0-6	2-6
1972	2.3138	0-5	2-5
1973	2.1339	0-6	2-6
1974	1.8871	0-6	2-6
1975	1.5931	0-8	2-8
1976	1.4942	0-6	2-6
1977	1.4363	0-6	2-6
1978	1.5324	0-6	2-6
1979	1.2241	0-5	2-5
1980	1.8381	0-4	2-4
1981	1.8962	0-3	2-3

[a]Ages used in calculating terminal F using MVUE.
[b]Mean from VPA results (see Ahrenholz et al. 1987).

procedure, which obtains the Chapman-Robson survival estimate (Seber 1973), has the desirable statistical properties of being minimum variance and unbiased (MVUE). When estimating the instantaneous total mortality rate (Z) from survival (S), Chapman and Robson (1960) provide a modified estimator:

$$Z^* = -\ln S - (n-1)(n-2)/[n(n+X-1)(X+1)] \quad , \qquad (1)$$

where $S = X/(n+X-1)$; n = sum of all menhaden from a cohort in the landings greater than a given age (usually greater than age-1); X = sum of product of coded age (e.g., 0 for age-2, 1 for age-3, etc.) with catch in numbers-at-age.

In addition to these VPA's, further estimates of population size at age-0.5 were made for year classes 1965 through 1981 based on different assumptions as to the catch of age-0 menhaden versus the landings of age-0 menhaden which are sampled at the plants. One of the reasons for raising this issue is the statement "[i]t is generally acknowledged [that] the fishing process will sometimes kill additional numbers of small fish" (AMAC 1982). Robert W. Smith, then President of Seacoast Products Inc., states in reference to catching of age-0 menhaden by purse-seine (letter to Joseph W. Grimsley, Secretary of North Carolina's Department of Natural Resources and Community Development, 6 April 1982) that "because of the small size of the fish, the rule of thumb is that as many fish are wasted as are landed." Furthermore, Chester (1984) has demonstrated that in the North Carolina fall fishery, when most age-0 fish are landed, there is a bias towards underestimating the numbers of age-0 fish in the landings. In both cases the question arose as to what possible effect the underestimation of age-0 fish in the catches might have on the conclusions of this and previous stock assessments. Hence, three sets of quarterly VPA's were conducted such that the number of age-0's estimated in the landings were multiplied by 1.5, 2, and 4 to reflect increasing levels of underestimation of age-0's in the estimated catch in numbers-at-age. Only estimates of population size and fishing mortality for age-0 fish are altered in this analysis.

Landings in the Atlantic menhaden fishery historically have depended primarily on age-1 and age-2 fish in terms of numbers (Fig. 3). However, there are exceptions. In 1961 and 1962 large landings of age-3 and age-4 fish, respectively, resulted from the large 1958 year class (note age-1 fish landed in 1959 and age-2 fish landed in 1960). In 1979, 1981, 1983, and 1984 landings of age-0 fish (or "peanuts") exceeded landings of age-1 fish (and age-2 fish as well in 1984). Most Atlantic menhaden landed by the North Carolina fall fishery are age-0 fish (Fig. 4), and late-season fishing (after the Virginia season closes in November) off North Carolina by boats from Virginia plants in 1983 and 1984 contributed significant numbers of age-0 fish to South Atlantic catches (Fig. 5). This increased dependence on age-0 fish relative to total landings (four of the last six years) has increased the concern about "growth overfishing" in the Atlantic menhaden fishery, a concept that refers to the trade off between catching greater numbers of younger and smaller fish or catching fewer numbers of older and larger fish. The trade off depends both on the rate of growth of individual fish and the natural mortality rate of the stock. This concept will be discussed in greater detail in the section on yield-per-recruit analyses.

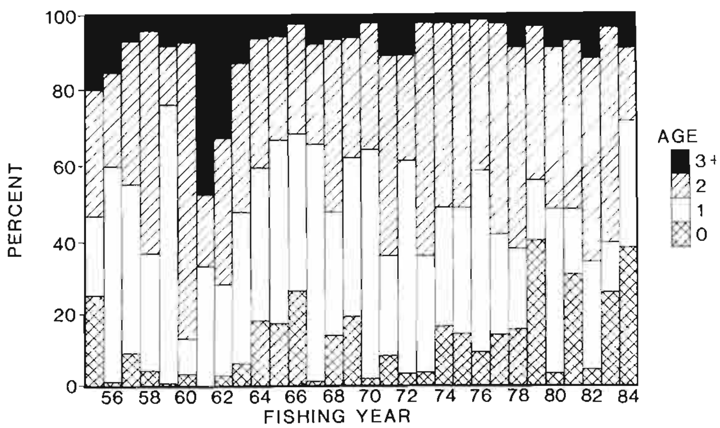

Figure 3
Contribution in percent of total numbers of Atlantic menhaden landed by age group for fishing years 1955-84.

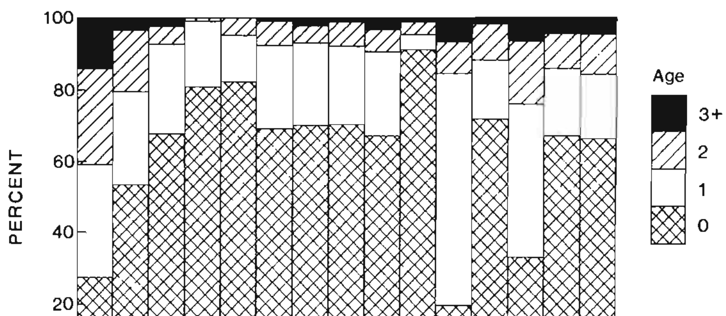

Figure 4
Contribution in percent of total numbers of Atlantic menhaden landed in the North Carolina fall fishery (Area 5) by age group for fishing years 1970-84.

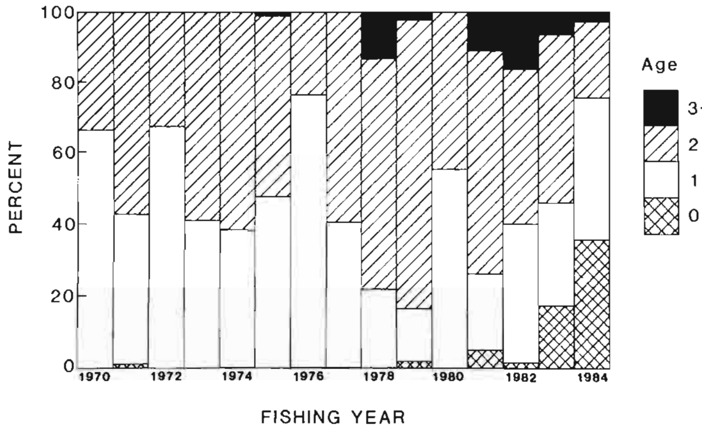

Figure 5
Contribution in percent of total numbers of Atlantic menhaden caught in the South Atlantic (Area 4) by age group for fishing years 1970-84.

Recruits to age-1 obtained from the second ("partial-quarterly") and third (quarterly) sets of VPA's for 1955-81 year classes range from 1.2 billion recruits in 1968 from the 1967 year class to 14.8 billion recruits in 1959 from the 1958 year class (Table 4). Recruitment was high for the 1956 and 1957 fishing years, exceptionally high for the 1959 fishing year, and low for the 1960-71 fishing years. Recruitment rose for the fishing years during the early 1970's, and has been generally high for fishing years since 1976, averaging over 5.7 billion recruits to age-1. Recent high recruitment values would seem to indicate a sufficient number of potential spawners and good survival prior to recruitment to the fishery. These implications will be discussed later in the section on spawner-recruit relationships. Similar trends are noted in recruitment to age-0.5 (f in Table 4 indicates the factor by which landings of age-0 fish have been multiplied). The effect of the multiplicative factor on estimates of recruitment to age 0.5 depends on the relative number of age-0 Atlantic menhaden in the landings for the year class (compare Table 4 with Figure 3). For instance, in 1961, when almost no age-0 fish were landed, no change is observed in the estimated recruitment to age 0.5 with increasing multiplicative factor, f. However, in 1979, when almost 40% of the menhaden landed were age-0 fish (f = 1.0), the estimate of recruitment to age-0.5 increases by over 50% for the multiplicative factor, f, equal to 4.0. Results would be expected to be similar for the 1984 year class.

Estimates of population size (based on age-1 and older Atlantic menhaden on 1 March) range from 2.1 billion fish in 1968 to 16.9 billion fish in 1959 (Table 5 and Fig. 6). The population size for the period 1976-82 averaged about 8.6 billion fish. This value is similar to those for population sizes between 1955 and 1961 (excluding the very large population size present in 1959).

Population exploitation rates (u, based on age-1 and older fish) ranged from 30% to 51% of the population removed by fishing each year (Table 5). Since 1975, the population exploitation rate has averaged 34% for age-1 and older fish, which is less than the average of 38% for 1955-82. Age-specific exploitation rates range from 16% to 89% removal of an age class for the fully recruited adult age classes (age-2 and older) (Fig. 7). Exploitation rates for age-1 Atlantic menhaden range from 13% to 40%, while the exploitation rates for age-0 (based on recruits to age-0.5) ranged from essentially 0% (in 1961) to 12% (in 1979). For fishing years 1955-81, an average 25% of age-1 fish and 65% of age-2 and older fish were taken by the fishery annually, with 30% and 20%, respectively, being lost to natural causes annually.

Table 4
Estimated number of Atlantic menhaden spawners that produced the year classes 1955-84, estimated egg production from the spawning stock, estimated numbers of recruits by year class at age-0.5 and age-1, and estimated egg production by the recruits.

	Spawners[a]		Recruits (10^9)					
			Age-0.5[b]					
Year class	No. (10^9)	Eggs (10^{12})	f=1.0	f=1.5	f=2.0	f=4.0	Age-1	Eggs (10^{12})
1955	1.89	214.0	7.87	8.29	8.71	10.40	5.60	52.4
1956	1.37	148.5	8.99	9.01	9.03	9.11	7.15	119.0
1957	0.72	84.9	4.42	4.59	4.75	5.42	3.26	55.1
1958	0.55	58.1	18.62	18.68	18.73	18.98	14.77	195.3
1959	1.30	89.1	2.72	2.73	2.74	2.76	2.16	33.2
1960	0.79	76.5	3.79	3.83	3.87	4.03	2.96	15.6
1961	2.96	155.8	2.77	2.77	2.77	2.77	2.21	13.9
1962	1.29	106.6	2.84	2.87	2.90	3.01	2.22	11.4
1963	0.43	37.4	2.30	2.36	2.41	2.63	1.75	8.0
1964	0.26	21.4	2.76	2.93	3.10	3.77	1.94	19.6
1965	0.19	13.8	2.07	2.21	2.35	2.92	1.43	10.0
1966	0.12	7.6	2.88	3.06	3.25	3.99	2.00	12.9
1967	0.21	17.0	1.52	1.53	1.53	1.54	1.21	13.8
1968	0.17	12.9	2.32	2.41	2.50	2.85	1.71	12.6
1969	0.14	10.5	3.45	3.53	3.62	3.98	2.61	24.2
1970	0.15	11.7	1.75	1.76	1.78	1.83	1.38	5.2
1971	0.21	15.0	4.54	4.58	4.62	4.79	3.56	5.8
1972	0.30	25.7	3.56	3.59	3.62	3.73	2.79	7.7
1973	0.08	7.0	3.94	3.97	4.01	4.14	3.10	10.5
1974	0.09	5.7	5.20	5.39	5.57	6.30	3.86	14.8
1975	0.12	7.1	9.07	9.24	9.41	10.10	6.96	23.2
1976	0.16	8.1	6.90	7.06	7.22	7.86	5.25	23.4
1977	0.25	12.2	6.60	6.88	7.17	8.31	4.81	22.2
1978	0.57	19.5	5.96	6.22	6.48	7.53	4.34	14.2
1979	0.53	18.8	10.38	11.25	12.13	15.63	6.88	26.2
1980	0.64	26.0	6.18	6.23	6.28	6.49	4.85	[c]
1981	0.52	20.8	9.51	10.19	10.88	13.63	6.49	[c]
1982	0.80	19.5	[c]	[c]	[c]	[c]	[c]	[c]
1983	0.51	16.7	[c]	[c]	[c]	[c]	[c]	[c]
1984	0.70	25.9	[c]	[c]	[c]	[c]	[c]	[c]

[a] Spawners present on 1 December prior to the year to which the year class was assigned (X.75 with $X>1$).
[b] Factor (f) by which landings of age-0 fish are multiplied in special virtual population analyses (see text).
[c] Not estimable (require data from 1985 and later fishing years).

Table 5

Annual estimates of Atlantic menhaden population size and catch in numbers (age-1 to maximum observed in millions), population exploitation rates (u), landings in thousands of metric tons, effort in vessel weeks (VW), population F, and proportion of age-0 fish in landings as numbers.

Year	Pop. size[a]	Catch (n)	u	Catch (10^3 MT)	Effort (VW)	Pop. F	Landings Age 0/0-8
1955	6,846.1	2357.4	0.344	641.4	2748	0.543	0.244
1956	8,192.4	3528.4	0.431	712.1	2878	0.736	0.010
1957	9,686.0	3212.1	0.332	602.8	2775	0.518	0.085
1958	7,012.4	2613.2	0.373	510.0	2343	0.603	0.039
1959	16,866.6	5342.2	0.317	659.1	2847	0.489	0.002
1960	9,047.0	2702.9	0.299	529.8	2097	0.454	0.026
1961	6,700.4	2598.1	0.388	575.9	2371	0.636	[b]
1962	4,514.8	2048.3	0.454	537.7	2351	0.793	0.025
1963	3,581.0	1667.6	0.466	346.9	2331	0.824	0.055
1964	2,777.4	1426.5	0.514	269.2	1807	0.958	0.175
1965	2,631.5	1260.4	0.479	273.4	1805	0.859	0.165
1966	2,149.5	991.2	0.461	219.6	1386	0.811	0.176
1967	2,598.5	977.2	0.376	193.5	1316	0.610	0.007
1968	2,097.3	993.7	0.474	234.8	1209	0.846	0.134
1969	2,280.7	710.0	0.311	161.6	995	0.477	0.182
1970	3,505.6	1381.5	0.394	259.4	906	0.650	0.015
1971	2,548.7	896.2	0.352	250.3	897	0.559	0.075
1972	4,486.3	1663.8	0.371	365.9	973	0.590	0.029
1973	4,339.3	1787.4	0.412	346.9	1099	0.691	0.030
1974	4,465.3	1675.1	0.375	292.2	1145	0.608	0.159
1975	5,415.7	1863.7	0.344	250.2	1218	0.543	0.138
1976	8,963.8	3009.2	0.336	340.5	1163	0.526	0.084
1977	8,628.6	3189.1	0.370	341.2	1239	0.597	0.132
1978	7,817.5	2627.8	0.336	344.1	1210	0.526	0.148
1979	7,278.2	2377.7	0.327	375.7	1198	0.508	0.386
1980	9,652.9	3244.0	0.336	401.5	1158	0.526	0.026
1981	8,421.6	2796.4	0.332	381.3	1133	0.518	0.298
1982	9,660.8	3061.6	0.317	382.4	948	0.489	0.036
1983	[c]	2977.7	[c]	418.6	995	[c]	0.245
1984	[c]	2253.8	[c]	326.3	892	[c]	0.365

[a]At start of fishing year on 1 March (X.0).
[b]Trace (0.0001).
[c]Not estimable.

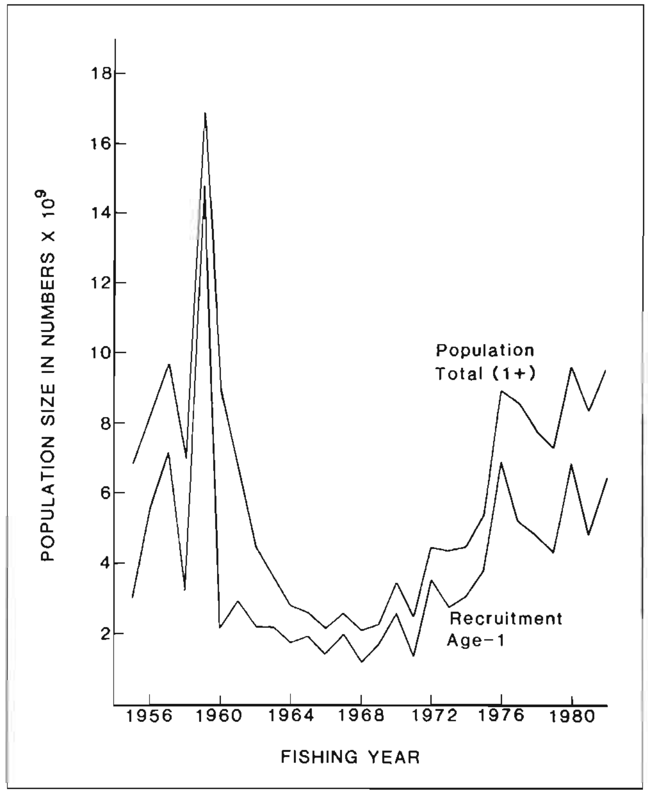

Figure 6

Population total (age-1 and older Atlantic menhaden) on 1 March and recruits to age-1 for fishing years 1955-82.

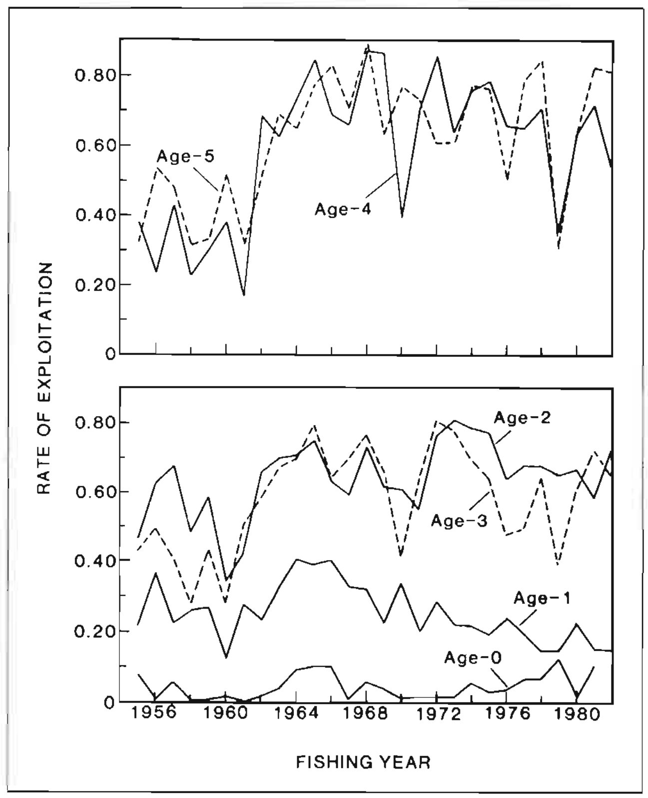

Figure 7

Estimates of annual rates of exploitation of Atlantic menhaden, ages 0-5.

Size-at-age and growth analyses

Estimates of length- and weight-at-age, summarized in Nicholson (1975) and Smith et al. (1987), are needed for estimating fishing yield, primarily from yield-per-recruit analyses. Estimates of length-at-age are also used to test an hypothesis concerning density-dependent growth (AMMB 1981) and to reconstruct potential egg production from spawners and recruits for use in developing spawner-recruit relations. Fork length (L_t, in millimeters) is estimated from age (t, in years) on the basis of the von Bertalanffy (1938) growth function,

$$L_t = L_{inf}(1 - \exp(-k(t - t_0))) \quad , \tag{2}$$

where L_{inf}, k, and t_0 are parameters to be estimated. The computer program BGC3 (Abramson 1971) was used to obtain parameter estimates for Eq. (2). This program employs a nonlinear regression algorithm (Vaughan and Kanciruk 1982). Weight (W_t, in grams) is then estimated from the weight-length relationship expressed in the linear form of the power function,

$$\ln W_t = a + b \ln L_t \quad , \tag{3}$$

where a and b are estimated parameters, and the bias from transforming from a normal to a lognormal variate (Miller 1984) is insignificant because of the small variance about the transformed variate. Annual estimates of a and b for fishing years 1970-84 were made (Table 6), with the percentage of variability explained by each of these annual regressions ranging from 98.0 to 99.4%. Estimates of a range from -11.3 to -12.6, and estimates of b range from 3.1 to 3.3. Based on these results, the weighted averages of these parameters were used in the following analyses when calculating weight from length ($a = -12.1$, $b = 3.2$).

Use of only coastwide estimates of mean length-at-age in size and growth analyses is inappropriate in an analysis of yield-per-recruit because of the distribution of Atlantic menhaden along the coast by age and size (Nicholson 1972, 1978b). Hence, mean lengths-at-age are calculated directly from the port sampling data by NMFS fishing area caught (e.g., North Atlantic, Middle Atlantic) and by season (or quarter, Table 2). These area-specific mean lengths-at-age are aligned by year class (or cohort) so that resultant growth curves represent the growth of a year class through its life span, rather than across several cohorts during a single fishing year. Mean lengths are assumed to represent the middle of the quarterly interval, so that age-X.125 is assigned for the mean length of the first quarter and so forth for the remaining quarters. Estimated parameters for the five NMFS fishing areas are given for year classes 1965-81 (Table 7), and are used to estimate fish length and weight at the start of each quarter by area (see section on yield-per-recruit analysis).

Corresponding coastwide estimates of the von Bertalanffy parameters were made for year classes 1965-81 by obtaining weighted averages of mean lengths-at-age across the five NMFS fishing areas (weighting based on catch in numbers-at-age for each area as in Ahrenholz et al. 1987). For those instances when the von Bertalanffy fitting procedure failed to converge, a linear regression of length (L) on age (t) was used. These growth curves are used only in the yield-per-recruit analyses, where they are appropriate only for interpolation within the range of ages from which the growth parameters were estimated. They are not appropriate for extrapolating beyond the range of ages for which data were available.

The size of age-0.5 and age-0.75 Atlantic menhaden were found by Ahrenholz et al. (1987) to be biased upwards. Therefore, we deleted lengths at these ages when fitting the von Bertalanffy growth equation to coastwide lengths-at-age for year classes 1965-81 (Table 8) for development of estimates of spawners and recruits as eggs (Table 4). In addition, we used fourth-quarter data from fishing area 5, as did Ahrenholz et al. (1987), to obtain parameter estimates for year classes 1955-64 (Table 8).

Estimates of annual weighted mean weights by age for Atlantic menhaden in purse-seine catches were calculated to indicate potential trends in yield-per-recruit that could be expected from the fishery (Fig. 8). These trends were affected by changes in fishing patterns both geographically and seasonally, so that part of the decline noted since 1970 is due to the shift of the center of fishing southward to smaller fish of the same age. Part of this decline can also be explained by the inverse relationship noted between first-year growth of Atlantic menhaden and year-class strength (AMMB 1981; Reish et al. 1985). Ahrenholz et al. (1983) obtained significant correlations for recruitment to age-0.5 with mean length at age-0.5 (Chesapeake Bay area) and with mean length at age-0.75 (North Carolina fall fishing area). Similar results have been obtained using data from the 1965-81 year classes, with 64% of the variability in lengths at age-0.5 from Chesapeake Bay area explained by population size (Fig. 9a), and 25% of the variability in lengths at age-0.75 from North Carolina fall fishing area explained by population size (Fig. 9b).

Table 6
Weight-length regression parameters for Atlantic menhaden, 1970-84 ($\ln W = \ln a + b \ln L$).

Year	ln a	b	r^2
1970	−11.712	3.151	0.994
1971	−11.436	3.092	0.993
1972	−11.690	3.133	0.992
1973	−11.313	3.070	0.980
1974	−11.795	3.156	0.988
1975	−11.908	3.180	0.991
1976	−12.419	3.279	0.991
1977	−12.618	3.319	0.992
1978	−12.361	3.270	0.992
1979	−12.498	3.296	0.992
1980	−12.474	3.293	0.993
1981	−12.582	3.309	0.992
1982	−11.689	3.148	0.985
1983	−11.621	3.125	0.992
1984	−11.554	3.121	0.987

Table 7

Area-specific von Bertalanffy parameters (includes 3rd- and 4th-quarter data from age-0 fish) for Atlantic menhaden, 1965-81. (These values *are not* suitable for general use—see text).

Year class	L_{inf}	K	$^*t_0$	n	Year class	L_{inf}	K	$^*t_0$	n
Area 1					**Area 4**				
1965	216.6	23.1	0*	5	1965	221.2	0.7641	−0.6596	8
1966	340.9	0.6286	−0.654	6	1966	27694.7	0.0011	−3.7288	7
1967	315.9	2.3476	1.1371	6	1967	109.0	34.7	0*	7
1968	334.1	0.9195	0.6251	5	1968	127.2	29.8	0*	8
1969	331.6	1.4831	0.7039	8	1969	75108.7	0.0006	−1.8791	9
1970	351.4	0.2773	−4.2640	6	1970	272.5	0.3233	−1.8040	7
1971	310.3	1.3572	1.1158	9	1971	94.1	49.8	0*	10
1972	297.6	1.0889	0.6424	8	1972	249.5	1.0191	0.2356	8
1973	318.9	0.4255	−1.2752	10	1973	198.1	3.3924	0.7673	6
1974	322.6	0.3752	−1.1375	12	1974	286.8	0.4411	−0.5467	9
1975	467.9	0.0935	−4.9384	13	1975	55233.0	0.0004	−5.8115	10
1976	330.2	0.3432	−0.9397	13	1976	314.6	0.3054	−0.5076	12
1977	317.6	0.5483	0.1540	12	1977	227.0	0.7426	0.1026	9
1978	299.2	0.5053	−0.7047	13	1978	117.1	27.4	0*	12
1979	447.0	0.1078	−3.9287	10	1979	283.6	0.3159	−0.6564	14
1980	312.0	0.4756	−0.1155	7	1980	222746.2	0.0002	−2.6669	11
1981	265.2	2.0023	1.4917	4	1981	276.8	0.4121	−0.3615	10
Area 2					**Area 5**				
1965	313.2	1.0060	0.4384	6	1965	407.4	0.3017	−0.5882	10
1966	348.6	0.5701	−0.3618	7	1966	371.7	0.4546	−0.1573	10
1967	353.5	0.4739	−0.5379	8	1967	382.3	0.4508	−0.0262	7
1968	429.0	0.1979	−2.7051	7	1968	163415.9	0.0004	−0.9768	8
1969	399.0	0.2903	−1.8364	9	1969	107.6	53.4	0*	8
1970	285.4	4.383	1.0415	7	1970	332.4	0.5331	−0.0235	8
1971	359.9	0.2831	−1.8545	9	1971	882.2	0.0814	−1.2732	6
1972	319.0	0.4460	−0.8359	9	1972	336.4	0.4772	−0.0614	6
1973	309.8	0.5135	−0.6848	11	1973	381.8	0.2691	−0.5751	8
1974	277.0	0.9954	0.8215	10	1974	328.9	0.4079	−0.0904	8
1975	435.4	0.1351	−2.8239	12	1975	394.5	0.2149	−1.0058	9
1976	315.4	0.4103	−0.6078	11	1976	375.1	0.2332	−0.7452	9
1977	11246.7	0.0011	−17.4552	7	1977	351.5	0.3118	−0.3058	9
1978	174.6	18.6	0*	8	1978	355.4	0.2575	−0.8781	10
1979	148.4	27.5	0*	7	1979	355.2	0.2682	−0.4681	10
1980	147.6	29.4	0*	7	1980	431.6	0.1814	−0.9713	9
1981	128.3	33.2	0*	7	1981	7522.8	0.0069	−1.3908	8
Area 3					**Coastwide**				
1965	483.3	0.1686	−1.7049	11	1965	592.4	0.1292	−1.4512	18
1966	345.8	0.4604	−0.7233	11	1966	421.7	0.2525	−0.9604	20
1967	429.7	0.2283	−1.3710	11	1967	502.6	0.1887	−0.9369	17
1968	477.3	0.1708	−1.9694	12	1968	1040.1	0.0539	−2.2117	18
1969	362.8	0.4493	−0.7612	11	1969	393.6	0.3117	−0.8714	19
1970	292.6	0.8165	−0.5528	8	1970	361.6	0.4248	−0.2902	17
1971	455.6	0.1898	−1.3816	10	1971	353.2	0.3701	−0.5432	19
1972	317.1	0.5361	−0.1293	10	1972	317.8	0.5630	−0.0034	18
1973	472.3	0.1779	−1.0721	11	1973	345.2	0.3607	−0.4743	22
1974	104194.1	0.0004	−2.4294	14	1974	348.3	0.3059	−0.7790	24
1975	353.0	0.2084	−1.3885	13	1975	392.1	0.2018	−1.1137	24
1976	252.8	0.4815	−0.7961	13	1976	359.2	0.2774	−0.4864	23
1977	279.0	0.3541	−1.0517	12	1977	389.9	0.2379	−0.6938	21
1978	225.2	0.6874	−0.6645	10	1978	360.5	0.2490	−0.8338	22
1979	245.2	0.3679	−1.4871	11	1979	520.9	0.1160	−1.3361	21
1980	215.5	0.8646	−0.2870	10	1980	1302.1	0.0371	−1.9474	17
1981	292.8	0.2760	−1.6498	10	1981	90.8	43.4	0*	15

*Von Bertalanffy model did not converge. MAREA input obtained from $L = a+bt$, t in years-of-age; a under L_{inf}, b under k, and 0 under t_0.

Table 8

Estimated von Bertalanffy growth parameters for Atlantic menhaden, year classes 1955-81 (general use estimates).

Year class	L_{inf}	K	t_0	n (means)
1955[a]	339.49	0.5401	0.1234	7
1956	343.67	0.4598	0.0245	7
1957	324.49	0.6260	0.0707	7
1958	363.73	0.3637	−0.1163	7
1959	355.64	0.3631	−0.4709	6
1960	354.69	0.4009	−0.1481	5
1961	340.52	0.4514	−0.3506	5
1962	376.35	0.4012	−0.1122	5
1963	370.04	0.3494	−0.4652	6
1964	331.17	0.6138	0.0606	5
1965[b]	421.17	0.2876	−0.4345	16
1966	371.75	0.4144	−0.1762	18
1967	377.20	0.4472	0.1676	16
1968	526.34	0.1679	−1.0108	16
1969	359.98	0.4923	−0.1047	17
1970	338.67	0.5948	0.1385	16
1971	344.49	0.4253	−0.2948	18
1972	317.80	0.5630	−0.0034	18
1973	334.14	0.4253	−0.1985	21
1974	326.53	0.4256	−0.1759	22
1975	380.03	0.2250	−0.8858	23
1976	339.80	0.3393	−0.1814	22
1977	361.79	0.3028	−0.3265	20
1978	362.65	0.2440	−0.8696	21
1979	547.63	0.1062	−1.4349	20
1980	894.42	0.0598	−1.6918	16
1981	764.67	0.0818	−1.2050	13

[a]Year classes 1955-64 represented by fitted values for 4th quarter, Area 5 (see Ahrenholz et al. 1987).
[b]Year classes 1965-78 represented by fitted values for weighted quarterly mean lengths.

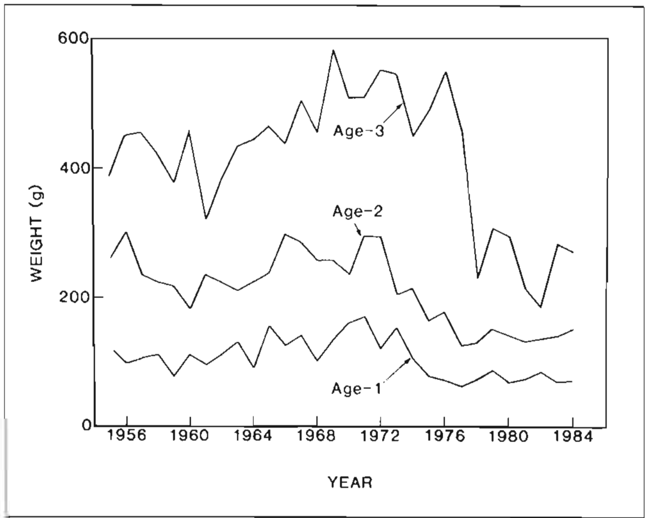

Figure 8
Weighted mean annual weight of purse-seine landed Atlantic menhaden, ages-1, 2, and 3, for fishing years 1955-84.

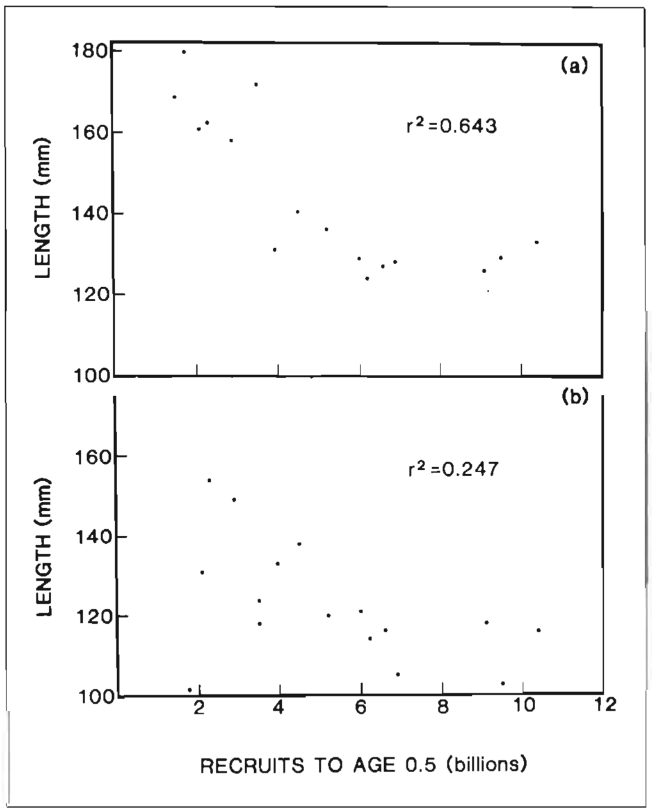

Figure 9
(a) Estimates of year-class recruitment at age-0.5 against mean length at age-0.5 (third quarter) for Atlantic menhaden caught in Chesapeake Bay area. (b) Estimates of year-class recruitment at age-0.75 against mean length at age-0.75 (fourth quarter) for Atlantic menhaden caught by North Carolina fall fishery.

Surplus production models

Surplus production models are typically used to obtain estimates of maximum sustainable yield (MSY) from yield and fishing-effort data (Vaughan et al. 1984). Ricker (1975) defines MSY as "[t]he largest average catch or yield that can continuously be taken from a stock under existing environmental conditions. (For species with fluctuating recruitment, the maximum might be obtained by taking fewer fish in some years than in others.)" When using surplus production models, catch-per-unit-effort is assumed to be proportional to population abundance and fishing effort proportional to fishing mortality. Theoretically, plotting catch against fishing effort should give a dome-shaped curve (Vaughan et al. 1984), which is not the case with Atlantic menhaden data (Fig. 10). When relating fishing effort (E) to the instantaneous fishing mortality rate (F), the catchability coefficient (q) is assumed to be constant; i.e.,

$$F = q E \ , \tag{4}$$

where the unit of fishing effort, E, is defined as vessel-weeks for Atlantic menhaden. As noted in Ahrenholz et al. (1987), the above unit of fishing effort, referred to as nominal effort, is not a reliable measure of fishing mortality. A unit of fishing effort that is a reliable measure of fishing mortality is referred to as "effective" effort. The difficulty in directly obtaining a reliable unit of fishing effort results from the schooling nature of menhaden, since menhaden and other schooling clupeids are more susceptible to fishing effort than non-schooling species [see discussion of "dynamic aggregation process" in Clark and Mangel (1979)].

To demonstrate that the population catchability coefficient, q, for Atlantic menhaden is not constant but dependent upon the population size, it was estimated by solving Eq. (4) for q ($=F/E$) for each fishing year from 1955 through 1982 (Fig. 11) and compared with the population size for the same fishing year (Fig. 12). To calculate the population instantaneous fishing mortality rate (F), it was first necessary to compute the population exploitation rate (u) by comparing numbers caught in a fishing year (for all ages 1-8) with the population size (for all ages 1-8) on 1 March for that year (Table 5). The population F is then calculated iteratively from

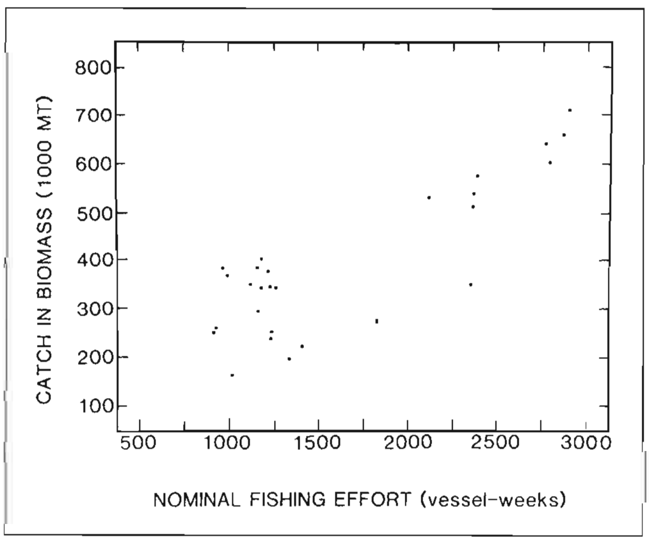

Figure 10
Atlantic menhaden landings (1000 metric tons) vs. nominal fishing effort (vessel-weeks) for fishing years 1940-84.

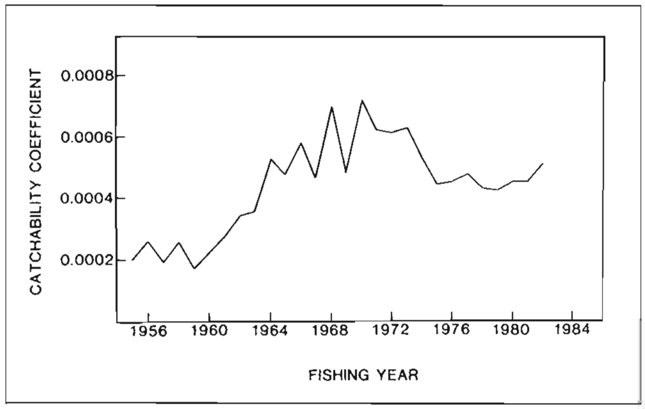

Figure 11
Catchability coefficient (fishing mortality per vessel-week) of Atlantic menhaden at age-1 and older for fishing years 1955-82.

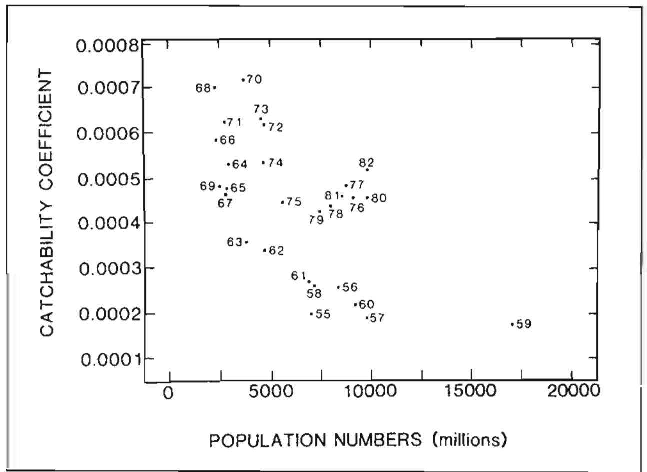

Figure 12
Estimates of the Atlantic menhaden population catchability coefficient (q) for fishing years 1955-82, plotted against the estimated population size (excluding age-0 fish).

the following equation:

$$F = u\,(F + M)/(1 - \exp(-(F + M))) \ , \tag{5}$$

where u and M ($=0.45$/year) are known. Estimates of q range from 0.00017·year·vessel-week in 1959 when the population size was 16.9 billion (age-1 and older fish) to 0.00072·year·vessel-week in 1970 when the population size was 3.5 billion. As noted in Ahrenholz et al. (1987), there is a pronounced inverse relationship between the catchability coefficient and population size (Fig. 12). Furthermore, the historical trend that they noted continues to be evident with the addition of three more years of data; that is, there appear to be two functional curves, 1955-69 and 1970-82. As described in Ahrenholz et al. (1987), the catchability coefficient increased beginning in 1959 with decreasing population size and an increasingly more efficient fleet due to various innovations. With increasing population size following 1971, the catchability coefficient declined to a level over twice that in 1959, which reflects the greater efficiency of the fleet in the 1970's and early 1980's compared with the 1950's and 1960's.

To adjust nominal fishing effort to account for variations in q, we calculated a mean value of q for the period 1955-82 (q_a) and adjusted nominal effort (E) so that q is made constant (q_a); i.e.,

$$E' = E\, q/q_a \ , \tag{6}$$

where E' is now a unit of "effective" fishing effort.

The computer program PRODFIT (Fox 1975), which accounts for nonequilibrium conditions, is used to estimate parameters for different surplus production models depending on the value of m in the following equation:

$$U = (A + B\,E')^{1/(m-1)} \ , \tag{7}$$

where U is catch-per-unit-effort, and A, B, and m are parameters to be estimated. The generalized production model of Pella and Tomlinson (1969) is obtained when m is allowed to be estimated freely. However, when m is forced equal to 2.0, the Schaefer model (Schaefer 1954, 1957) is obtained; when m is forced equal to 1.0, the Gompertz model (Fox 1970) is obtained. The program PRODFIT also allows the analyst to enter the number of significant age classes to be entered in the analysis (i.e., this is used in estimating parameters under nonequilibrium conditions). Those age classes contributing at least 10% to the landings in numbers served as the basis for determining the number of significant age classes for each fishing year in the analysis (1955-82). Estimates of MSY range from 448.9 kmt when m is forced equal to 2.0 (Schaefer model) to 459.3 kmt when m is estimated freely (1.59; Pella-Tomlinson model).

Ahrenholz et al. (1987) suggested a more direct method by utilizing estimates of population F for the independent variable instead of adjusting fishing effort. Using this approach, estimates of MSY range from 455.4 kmt at $F = 0.53$ when m is forced equal to 2.0, to 487.2 kmt at $F = 0.42$ when m is estimated freely (1.33) (Fig. 13). Since 1975, population fishing mortality rates have averaged 0.53 (Table 5) and observed landings have averaged 356 kmt.

With MSY estimates ranging about 470 kmt, one would expect that this level of landings could be obtained with current levels of vessel and plant capacity. However, changes in fishing patterns since the 1950's and loss of reduction plants primarily to the north restrict the industry's ability to attain MSY. The next section provides some insight into whether there is sufficient spawning stock to guard against recruitment failure or whether there are sufficient numbers of recruits to sustain the stock.

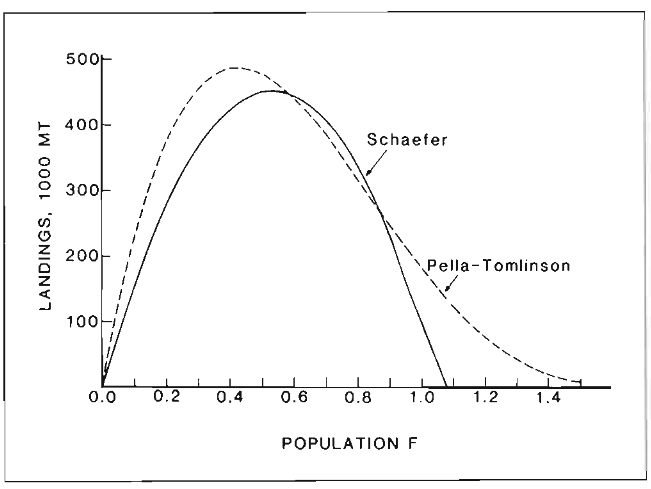

Figure 13

Catch of Atlantic menhaden in thousands of metric tons against estimates of population F for fishing years 1955-82. Solid curve is the parabolic (Schaefer) production model, and dashed line is the Pella-Tomlinson generalized production model.

Spawner-recruit relationships

An important question in population dynamics and in fisheries management concerns the degree of dependency between the number of spawners and the number of subsequent recruits to the stock. If there is no such dependency, then there is little that a manager can do to control the number of recruits (and hence future stock sizes) other than to assure sufficient spawners to produce subsequent recruits to the population and to preserve the quality of the habitat utilized by prerecruit larvae and juveniles. If there is a quantifiable relationship between spawners and recruits, then management can be designed to maximize the landings based on this relationship. Such a relationship was examined using the Ricker (1954) model (Schaaf and Huntsman 1972; Nelson et al. 1977; Schaaf 1979; Reish et al. 1985; Ahrenholz et al. 1987).

Estimation of the number of recruits to age-0 (for four multiplicative factors: $f = 1.0$, 1.5, 2.0, and 4.0) and to age-1 has been described in the section on virtual population analyses (Table 4). Estimation of spawners follows the description given in Ahrenholz et al. (1987). The number of mature spawners for each fishing year is given by age (Table 9), where peak spawning is assumed to occur during the fourth quarter (between 1 December and 29 February) of each fishing year (hence the use of age-X.75). The total number of spawners for each recruitment year is given by the sum from age-2.75 through age-8.75 (Table 4).

Indices of spawners and recruits have also been estimated as potential egg production. Estimates of egg production as a function of fish length were obtained from the equations used by Nelson et al. (1977) which were derived from data in Higham and Nicholson (1964). Ahrenholz et al. (1987) used the same expression:

$$\ln(EGGS) = 0.315 + 0.0176\, L \ , \tag{8}$$

where $EGGS$ equals thousands of eggs produced per female, and L equals estimated fork length (mm). Mean length-at-age for the third quarter (Table 10) was calculated from the von Bertalanffy growth curves given in Table 8. To fill in missing values, we used either the observed mean length-at-age for the fourth quarter or the means from the adjacent three year classes. The expected egg production per female of a given age was calculated using Eq. (8) and the lengths given in Table 10. Assuming a 50:50 sex ratio, multiplying population numbers-at-age (Table 9) by one-half, the expected egg production per female-at-age gives the potential egg production per individual-at-age (Table 11). Summing across ages for the same fishing year gives the numbers of spawners as potential eggs (Table 4). Summing across ages for the same year class (or cohort) gives the numbers of recruits as potential eggs; i.e., recruits as eggs for a year class are calculated from the number of eggs estimated as actually produced by that year class during its lifetime (Table 4). The number of eggs produced by a year class does not differ, whether referring to recruits to age-0.5 or age-1, or referring to recruits based on the increasing multiplicative factor.

Table 9

Estimates of spawning stock size (10^3) for Atlantic menhaden, 1954-81 seasons, at start of 4th quarter (resultant year class is year +1).

	Age in years						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75
1954[a]	717,088.4	976,389.5	141,718.5	43,441.7	10,451.6	2,689.0	[b]
1955	750,544.7	218,095.6	329,260.0	52,045.7	13,751.9	3,463.6	931.0
1956	284,846.4	213,233.7	103,337.2	101,485.8	12,174.1	3,589.2	593.9
1957	315,980.1	98,471.5	72,620.9	35,778.3	21,458.0	1,817.2	1,016.6
1958	1,060,636.0	141,757.4	45,782.9	29,083.3	11,453.0	6,505.8	433.1
1959	330,978.0	366,103.3	63,751.7	19,264.4	7,895.4	2,366.1	1,973.7
1960	2,660,856.3	144,374.9	124,950.2	19,006.9	5,398.5	1,352.8	866.0
1961	433,025.0	736,605.6	69,969.6	46,336.2	5,792.6	1,203.7	153.2
1962	216,040.7	84,780.9	98,030.7	19,041.5	6,568.7	1,250.8	200.0
1963	173,767.0	43,462.7	18,212.7	15,720.6	2,790.7	985.3	197.9
1964	151,144.3	26,765.7	4,380.3	2,345.2	1,118.1	177.3	190.0
1965	101,328.0	12,859.4	1,425.9	176.7	265.5	56.4	25.2
1966	194,344.5	18,778.4	1,407.3	18.6	25.4	80.3	7.0
1967	133,382.8	36,082.5	2,859.1	210.4	2.2	0	0
1968	121,343.1	16,252.6	1,270.9	199.1	10.0	0	0
1969	124,839.7	26,039.2	772.1	41.5	1.2	0	0
1970	174,942.4	33,984.2	5,670.2	55.0	0	0	0
1971	263,705.9	28,407.7	3,879.2	446.6	0	0	0
1972	60,802.2	13,899.5	699.9	620.1	0	0	0
1973	84,517.1	3,904.4	2,005.3	125.9	0	0	0
1974	106,351.6	10,127.0	344.3	142.6	0	0	0
1975	144,107.8	15,026.2	617.9	22.8	7.4	0	0
1976	214,064.8	37,623.1	2,234.4	162.0	0	0	0
1977	507,498.8	58,255.5	5,320.5	130.4	8.0	0	0
1978	429,083.4	87,302.1	13,136.7	732.1	0	0	0
1979	470,146.6	139,849.9	30,565.0	2,486.7	11.6	0	0
1980	382,506.6	93,321.7	32,021.3	7,390.2	727.9	0	0
1981	751,194.3	36,971.6	8,452.4	889.5	1,911.0	0	0
1982	361,689.3	138,577.5	12,155.3	1,319.1	127.3	948.0	0
1983	507,265.7	126,378.8	61,097.6	2,375.1	59.6	0	604.5

[a]Derived from 1 March 1953 estimate (Ahrenholz et al. 1987).
[b]Not estimable.

Spawners as numbers of adults on 1 December (Table 4) ranged between 76.0 million in 1972 (producing the 1973 year class) and 2,956.8 million in 1960 (producing the 1961 year class). Spawners as potential eggs on 1 December ranged between 5.7 trillion eggs in 1973 (producing the 1974 year class) and 214.0 trillion eggs in 1954 (producing the 1955 year class). Low spawning stock size was the rule from 1964 to 1977, and a medium-to-high spawning stock size from 1955 to 1963 and 1978 to 1984. High recruitment in 1958 resulted in large spawning stocks in 1960 (as age-2 fish) and in 1961 (as age-3 fish). High recruitment in 1952 and 1956 resulted in large spawning stocks (as age-2 fish) in 1954 (producing the 1955 year class) and 1958 (producing the 1959 year class). During the late 1950's and early 1960's, the contribution of late age-2 spawners to the spawning stock was highly variable, ranging between 35% and 90% in numbers and between 20% and 75% as eggs (Fig. 14). Since the mid-1960's, the contribution of late age-2 spawners to the spawning stock has averaged about 80% in numbers and about 70% as eggs.

Parameters of the Ricker model were estimated by nonlinear regression from the following equation:

$$R = aS \exp(-bS) \;, \qquad (9)$$

where R equals recruits (numbers at age-0.5 or age-1 or potential eggs), S equals spawners (number of adults or potential eggs), and a and b are parameters to be estimated. Six regressions were calculated from the data presented in Table 4. Five regressions were calculated using spawners in numbers versus the five indices of recruits in numbers (four multiplicative factors for recruits to age-0.5 and also recruits to age-1). An additional regression was calculated with both spawners and recruits as potential eggs. In all cases, parameter estimates for both a and b were significantly greater than zero, indicating a statistically significant relationship. These parameters do not vary appreciably with increasing multiplicative factor based on recruits to age-1. Parameter a increases from 29 to 32, and parameter b increases from 0.0014 to 0.0015 while increasing the multiplicative factor from 1 to 4. Depending on the level of the multiplicative factor (f), estimates of maximum recruitment to age-0.5 obtained from spawner-recruit relations based on spawners and recruits to age-5 in numbers range from 7.6 (f = 1) to 9.0 (f = 4) billion menhaden. This range of estimates is similar to estimates of mean recruitment to age-0 for the period 1976-81, ranging from 7.6 (f = 1) to 9.9 (f = 4) billion menhaden. Increasing the number of age-0 menhaden presumed killed (increasing f), results in an increase in the estimated fishing mortality rate for age-0 menhaden during the third and fourth quarters and in the estimated recruits to age-0.5 (but not age-1).

Table 10

Estimated mean length-at-age for Atlantic menhaden spawning stock by year (year class produced is tabular year +1).

	Age in years						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75
1954[a]	264.3	299.3	309.5	315.8	318.1	327.8	-
1955	268.4	297.0	306.5	316.8	321.0	327.8	338.0
1956	267.2	297.8	307.8	312.1	312.7	326.2	315.0
1957	257.3	303.2	314.2	318.5	320.5	326.0	340.0
1958	245.5	291.6	314.8	322.2	329.6	331.0	341.0
1959	263.9	281.7	311.6	323.1	327.4	329.5	341.0
1960	235.5	292.1	304.5	323.2	328.3	335.3	342.0
1961	245.2	274.6	307.2	319.0	330.0	334.4	338.6
1962	243.7	278.8	301.8	315.2	328.1	334.0	338.6
1963	256.3	280.4	302.2	320.7	319.5	333.8	336.3
1964	257.0	287.0	304.9	318.5	333.8	321.8	337.5
1965	249.7	269.4	306.5	321.4	329.8	342.9	323.1
1966	267.6	285.2	322.8	318.8	332.4	337.7	349.3
1967	252.6	296.8	310.2	340.5	326.7	-	-
1968	261.2	294.8	312.5	327.9	352.4	-	-
1969	258.3	298.7	326.4	321.1	340.3	-	-
1970	246.4	301.2	323.5	350.1	-	-	-
1971	271.7	289.7	328.6	339.9	-	-	-
1972	267.0	306.0	326.2	346.1	-	-	-
1973	250.1	299.1	327.0	357.2	-	-	-
1974	250.4	282.8	316.9	339.8	-	-	-
1975	238.8	279.4	304.2	326.6	347.7	-	-
1976	232.5	271.8	295.9	318.1	-	-	-
1977	212.3	265.1	293.4	305.3	327.3	-	-
1978	214.1	246.1	286.4	307.5	-	-	-
1979	219.2	250.3	273.1	300.3	316.7	-	-
1980	212.7	256.5	276.0	294.6	309.4	-	-
1981	196.4	245.2	284.0	294.4	311.8	-	-
1982	208.5	231.8	270.6	304.3	307.4	325.6	-
1983	211.3	248.3	263.6	290.6	319.3	-	336.5

[a]Estimated mean lengths-at-age for years 1954-64 from Ahrenholz et al. (1987).

Table 11

Potential egg production (10^{12}) by year, 1954-83, for Atlantic menhaden by age (resultant year class is year +1).

	Age in years						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75
1954	51.46	129.74	22.53	7.72	1.93	0.59	0
1955	57.90	27.83	49.68	9.41	2.68	0.76	0.24
1956	21.51	27.59	15.95	16.89	2.05	0.77	0.10
1957	20.05	14.01	12.54	6.67	4.14	0.39	0.28
1958	54.68	16.45	7.99	5.78	2.59	1.51	0.12
1959	23.59	35.69	10.52	3.89	1.72	0.53	0.55
1960	115.03	16.90	18.19	3.85	1.19	0.34	0.24
1961	22.20	63.37	10.68	8.71	1.32	0.30	0.04
1962	10.79	7.85	13.61	3.35	1.45	0.30	0.04
1963	10.83	4.14	2.55	3.04	0.53	0.24	0.05
1964	9.54	2.86	0.64	0.44	0.27	0.03	0.05
1965	5.62	1.62	0.22	0.03	0.06	0.02	0.01
1966	14.78	1.95	0.28	[a]	0.01	0.02	[a]
1967	7.79	4.59	0.46	0.06	[a]	0	0
1968	8.25	2.00	0.21	0.04	[a]	0	0
1969	8.06	3.42	0.16	0.01	[a]	0	0
1970	9.16	4.69	1.15	0.02	0	0	0
1971	21.56	3.19	0.86	0.12	0	0	0
1972	4.58	2.08	0.15	0.19	0	0	0
1973	4.72	0.52	0.43	0.05	0	0	0
1974	5.98	1.01	0.06	0.04	0	0	0
1975	6.60	1.41	0.09	0.01	[a]	0	0
1976	8.78	3.08	0.28	0.03	0	0	0
1977	14.58	4.24	0.64	0.02	[a]	0	0
1978	12.73	4.55	1.39	0.11	0	0	0
1979	15.26	7.84	2.56	0.34	[a]	0	0
1980	11.07	5.84	2.82	0.90	0.12	0	0
1981	16.32	1.90	0.86	0.11	0.32	0	0
1982	9.72	5.61	0.97	0.19	0.02	0.20	0
1983	14.23	6.84	4.33	0.27	0.01	0	0.15

[a]Trace (<0.005).

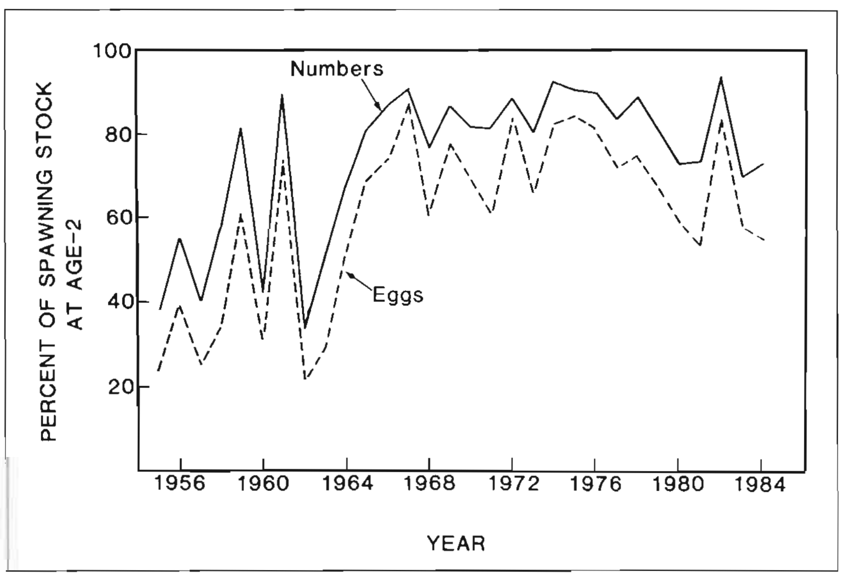

Figure 14

Contribution of late age-2 spawners (%) to total spawning stock (numbers) and to total egg production (eggs) of Atlantic menhaden for fishing years 1955-84.

As illustrated in Fig. 15 for the Ricker curve based on spawners in numbers and recruits to age-1, considerable scatter (or unexplained variability) remains due to environmental conditions or measurement error. Given the scatter evident from these regressions, their use is of limited value; e.g., not useful for predicting future absolute population sizes. However, these relationships are statistically significant, so that the number of future recruits does depend to some extent upon the size of the spawning stock which produced them, consisting primarily of late age-2 spawners since the late 1960's (Fig. 14).

Hence, although recruitment has been high since the late 1970's, it potentially depends largely upon environmental conditions (as evidenced in part by the unexplained scatter in Fig. 15) which are usually beyond the control of management. To the extent that recruitment does depend upon the spawning stock, the dependency has rested since the late 1960's primarily on late age-2 spawners. The concern of management is that several poor environmental years leading to several poor recruitment years could put the Atlantic menhaden population at risk. Thus, there is need to increase the proportion of older fish (age-3 and older) in the spawning stock.

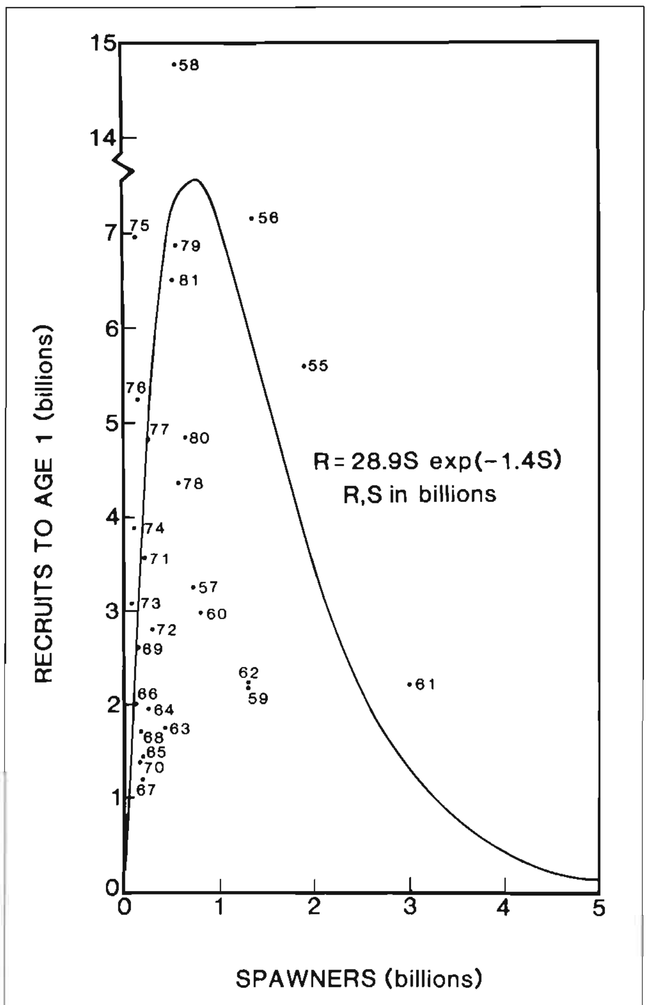

Figure 15

Numbers of Atlantic menhaden recruits (*R*, in billions) plotted against numbers of spawners (*S*, in billions) for year classes 1955-81. Curve represents the fitted Ricker function.

Yield-per-recruit analyses

The yield-per-recruit approach compares the rates of growth and mortality (natural and fishing) to determine whether the same yield is obtained from the fishable population as can be given the observed number of recruits. Yield-per-recruit is simply the expected yield in biomass from a year class or cohort (surviving fish from all spawning that occurs in a given year) during its fishable life span divided by the initial size of the cohort in numbers (i.e., recruits).

The computer program employed in this analysis (MAREA, Epperly et al. 1986) was modified from a multiple-gear extension (MGEAR, Lenarz et al. 1974) of the Ricker-type yield-per-recruit model to accommodate a multiple-area fishery, and utilizes area-specific estimates of growth (based on von Bertalanffy growth equations summarized in Table 7) and fishing mortality rates obtained from virtual population analysis. Ricker (1975) subdivided the exploited phase into a number of segments during which mortality and growth rates can be assumed constant. Ricker's approach permits instantaneous natural and fishing mortality rates to vary during the fishable life span and permits a general growth pattern to be used. Total equilibrium yield-per-recruit is then obtained by summing the catches in each segment over the total number of segments in the fishable life span.

Several assumptions inherent to yield-per-recruit modeling (Vaughan et al. 1984) are accounted for in this analysis. First, although the entire Atlantic menhaden stock is included in our analysis, the computer program MAREA permits the estimation of area-specific yield-per-recruit. Second, the poor relationship of spawners to recruits suggests that mortality is relatively independent of population density and will not significantly impact on our yield-per-recruit analysis. Finally, the use of the multiplicative factor to increase numbers of age-0 fish, so as to adjust for those age-0 fish killed but not landed during the purse-seine operation, will in part account for the lack of perfect retention by fishing gear above a critical size or age (knife-edge selection).

The end product of a yield-per-recruit analysis for fisheries management is an isopleth diagram which presents the yield-per-recruit for different ages at entry to the fishery and instantaneous fishing mortality rates (*F* or *F*-multiples). An example is shown for estimated growth and mortality rates for the 1981 fishing year (Fig. 16). Yield-per-recruit for this fishing year is 46.0 g with an age at entry of 0.5 years and *F* multiple of 1.0/year (Table 12). A goal of the fishery manager from a biological perspective is to maximize the yield-per-recruit for a fishery, while allowing sufficient recruitment to maintain stock. When natural mortality is large compared with the growth rate of an individual fish, then the cohort biomass decreases with time, and fish should be caught at a relatively young age. Conversely, when natural mortality is small compared with the growth rate of an individual fish, then the cohort biomass increases with time, and the age-at-entry to the fishable stock should be delayed. Usually the rate of growth declines with age so that there is an intermediate age such that cohort biomass is at a maximum. The isopleth diagram permits a comparison of the total yield from fewer, larger fish to that from more, smaller fish based on the same number of recruits to the year class. Hence, the manager may consider various strategies for attaining maximum yield-per-recruit by altering the age-at-entry or the instantaneous fishing mortality rate.

Estimates of yield-per-recruit for Atlantic menhaden have been calculated using MAREA for the fishing years 1976-81 (the years 1976-78 have been averaged to permit comparison with estimates

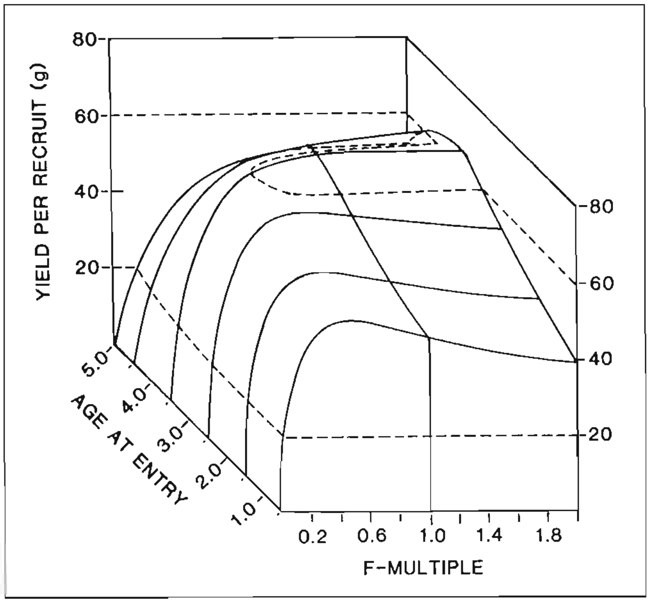

Figure 16

Overall yield-per-recruit of Atlantic menhaden under current conditions (*F*-multiple of 1.0 and age-at-entry of 0.5) using average fishing mortality values by quarter for the 1981 fishing season.

Table 12

Estimates of yield-per-recruit for Atlantic menhaden for the years 1976-81 by age-at-entry to the fishery and *F*-multiple. For each year yield-per-recruit given in grams for actual conditions (age-at-entry = 0.5; *F*-multiple = 1.0); remaining values are percent change from yield-per-recruit estimates.

Age-at-entry	*F*-multiple 0.2	0.6	1.0	1.4	1.8
Mean 1976-78 fishing years					
0.5	−13.3	+6.0	58.62 g	−6.2	−11.2
1.0	−12.6	+9.2	+4.9	+0.1	−3.8
2.0	−11.8	+15.6	+15.0	+13.1	+11.6
3.0	−21.8	+21.1	+29.5	+31.9	+32.7
1979 fishing year					
0.5	−32.0	−0.2	53.04 g	−4.6	−9.7
1.0	−31.1	+6.1	+11.1	+10.2	+8.1
2.0	−31.9	+8.8	+16.9	+18.4	+18.4
3.0	−49.7	−7.2	+7.7	+14.4	+18.0
1980 fishing year					
0.5	−18.2	+4.1	53.84 g	−5.5	−10.2
1.0	−18.1	+4.7	+0.9	−4.4	−8.9
2.0	−17.0	+13.0	+14.3	+13.0	+11.7
3.0	−27.6	+14.3	+24.8	+28.7	+30.6
1981 fishing year					
0.5	−3.3	+9.3	45.95 g	−7.3	−12.6
1.0	−1.8	+15.2	+8.6	+3.4	0.0
2.0	−1.5	+18.4	+12.7	+7.6	+4.1
3.0	−2.4	+36.4	+40.6	+41.0	+41.0

by Ahrenholz et al. 1987). During these fishing years, yield-per-recruit ranged from 46 g in 1981 to 59 g for the period 1976-78. In general, yield-per-recruit increases with increasing age-at-entry up to age-3 fish. Greater yield-per-recruit would be obtained for an *F*-multiple of 0.6 (60% of fishing mortality rate for that fishing year) with an age-at-entry of 0.5 years than at the current levels of *F* and age-at-entry. Maximum yield-per-recruit for the range of ages-at-entry and *F*-multiples given occurs at age-3 and an *F*-multiple of 1.8. Fishing year 1979 is an exception to these general statements. Gains from increasing the age-at-entry to 1.0 year (eliminate the harvest of age-0 fish) range from 0.9% in 1980 (when very few age-0 fish were landed; Fig. 3) to 11.1% in 1979 (when record numbers of age-0 fish were landed). Changes in yield-per-recruit are more variable when reducing fishing mortality by 40% (i.e., *F*-multiple=0.6), ranging from a loss of 0.2% in 1979 to a gain of 9.3% in 1981.

Yield-per-recruit declines with increasing numbers of age-0 menhaden killed by the fishing fleet compared with estimated as landed (multiplicative factor, *f*) (Table 13). However, greater gains from increasing age-at-entry to the fishable stock are available than suggested in Table 12. When large numbers of age-0 menhaden were landed in 1979 and 1981 (Fig. 3), the decline in yield-per-recruit with increasing multiplicative factor was most pronounced. When few age-0 menhaden were landed in 1980, the decline in yield-per-recruit with increasing multiplicative factor was insignificant (53.8 to 52.5). Changes in availability of age-0 menhaden can vary significantly from year to year, depending on the timing of juvenile migrations out of nursery areas in the late fall. Hence, gains in yield-per-recruit from raising the age-at-entry to the fishable stock will also vary significantly from year to year.

A series of MAREA computer runs was made for each fishing year from 1970 through 1981. The decline in yield-per-recruit (Fig. 17) since 1970 can be attributed largely to a comparable decline in the average weight of fish landed during this period (Fig. 7). The decline of the Atlantic menhaden fishery in the North and Middle Atlantic areas and increased importance of fishing farther south has led to an increased dependence on younger and smaller fish (Fig. 8). Especially important is the increased dependency on age-0 fish in the North Carolina fall fishery (Fig. 4).

Table 13

Yield-per-recruit from the Atlantic menhaden fishery for fishing years 1976-81 and by multiplicative factor increasing the number of age-0 menhaden assumed caught or killed by the purse-seine fleet.

Fishing year	Multiplicative factor 1.0	1.5	2.0	4.0
1976-78	58.6	57.3	56.1	52.1
1979	53.0	50.8	48.9	43.2
1980	53.8	53.6	53.4	52.5
1981	45.9	44.4	43.0	38.8

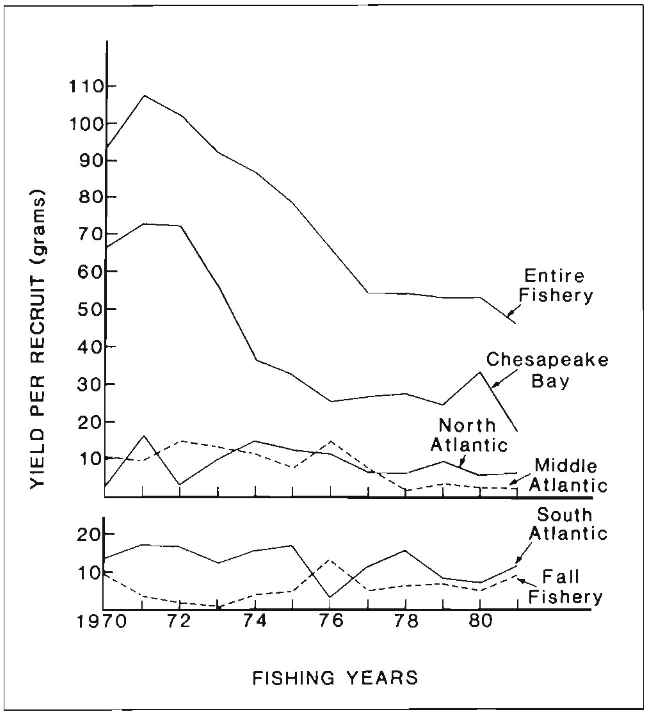

Figure 17
Estimated yield-per-recruit of Atlantic menhaden for fishing patterns and growth prevalent during fishing years 1970-81.

Management implications

Although landings have recovered somewhat from the depressed levels during the 1970's, they have not returned to the levels attained during the late 1950's when they averaged 625 kmt during the 1955-59 fishing years (Fig. 2). Even though estimates of MSY of 450-490 kmt at a population F of 0.5/year were obtained from the surplus production models (Fig. 13), those levels are unlikely to be attained over an extended period given the present structure of the fishery. However, recent landings averaging 356 kmt with a population F averaging 0.53/year since 1975 raises the question why MSY has not been attained. Estimates of MSY from the surplus production approach represent an historical average. Cycles or patterns of recruitment within this historical period (Table 4) suggest that greater yields than MSY are available at times, and smaller yields than MSY are available at other times. The crux of the problem for management is associated with predicting in advance the level of recruitment (primarily controlled by environmental factors) so that management and the fishing fleet can respond appropriately. Such a predictive tool is not yet available for Atlantic menhaden.

As discussed in the section on spawner-recruit relationships, sufficient recruitment has been available since 1975 to attain MSY. Since considerable scatter about the fitted spawner-recruit curves exists (Fig. 15), it appears that managing the fishery to maintain large numbers of spawners would prove fruitless and that environmental conditions may outweigh the availability of spawners in controlling subsequent recruitment. However, the Ricker spawner-recruit relationships are marginally significant, and combined with the great importance of late age-2 spawners to the spawning stock (Fig. 14) they suggest that increasing the number of older (age-3+) spawners would aid in guarding against a possible stock collapse brought on by heavy fishing during a period of poor recruitment.

While parameters obtained from the Ricker model for spawners and recruits to age-0.5 vary little in numbers with increasing multiplicative factor, estimated recruits to age-0.5 range from 7.6 to 9.0 billion fish. When multiplied by the average coastwide yield-per-recruit (1976-81) with an age-at-entry of 0.5 (54.8-48.5 g.) (Table 13), a rough estimate of yield from recent cohorts ranges from 416.2 to 436.3 kmt, depending on the level of the multiplicative factor. Similarly, multiplying mean recruitment for the same period (1976-81) by average coastwide yield-per-recruit provides a range in estimated yield of 415.7 to 480.6 kmt. The range of MSY estimates from the surplus production approach (450 to 490 kmt) is slightly greater than the range in estimated yields based on maximum recruitment from the spawner-recruit relationships, and overlaps the range based on the mean of recent recruitment. The upper end of the estimated ranges using recruitment assumes 2 to 4 times as many age-0 menhaden were killed than estimated as landed.

The decline in yield-per-recruit since 1970 (Fig. 17) has been attributed largely to the decline in average weight-at-age of fish landed during this period (Fig. 8). The general shift in activity of the fishery to more southern waters (Chesapeake Bay and South Atlantic areas and the North Carolina fall fishery) also explains some of the observed decline (Fig. 1). Since 1976, however, no trend in yield-per-recruit is obvious. In general, increasing the age-at-entry causes an increase in the yield-per-recruit, except for small F-multiples; e.g., F-multiple = 0.2 (Table 12). On the other hand, decreasing the F-multiple to F-multiple = 0.6 generally causes a decrease in yield-per-recruit, except for the 1979 fishing year. Greater declines or any increases in the F-multiple generally cause a decrease in yield-per-recruit at the current age-at-entry. If greater numbers of age-0 menhaden are killed than estimated as landed (multiplicative factor greater than one), then current levels of yield-per-recruit are lower, and greater gains in yield-per-recruit are available by raising the age-at-entry to the fishable stock. Gains in yield-per-recruit depend on the year-to-year availability of age-0 menhaden, which varies with the timing of migration by juveniles from their nursery areas in the late fall. These results suggest that the fishery is harvesting the Atlantic menhaden stock at too young an age, and that the age-at-entry should be raised to increase potential yield from the stock.

In summary, the modern fishery has a high dependency on prespawners (age-2 and younger fish), so large fluctuations in year-to-year availability and catches are to be expected. To increase yield and enhance the stability of the resource, it is desirable that the number of age classes significantly contributing to the fishery be increased. This would create a buffer against future poor recruitment years and lessen the year-to-year fluctuations in landings. Furthermore, greater yields should be attainable from the stock. Whether MSY estimates of 450-490 kmt are attainable may be questioned because of changes in plant locations and fishing patterns. However, gains in yield-per-recruit are possible by adjusting the age-at-entry.

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