

Consideration of Uncertainty in Stock Assessment of Atlantic Menhaden

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Abstract.—Stock assessments of Atlantic menhaden are conducted annually for the Atlantic States Marine Fisheries Commission, as required by the recently updated Fishery Management Plan, adopted in 1992. Uncertainties in stock assessments have been explored over the years from many perspectives. Two general areas of analysis are considered here. The first area is largely deterministic and concerns the virtual population analysis (VPA), including development and coherence of the catch-at-age matrix; historical retrospective problems; implications of assuming constant M at all ages analyzed; and reliability of recruitment estimates relative to fishery-independent juvenile abundance indices when used for calibrating the VPA. The second area of consideration comprises stochastic analyses, including stochastic projections based on biological benchmarks determined from yield-per-recruit and spawning-stock-biomass-per-recruit models; bootstrapped application of a surplus-production model; and projections from that production model. Nonetheless, the largest uncertainty in assessment of the stock stems not from modeling considerations, but is a biological question: Can the high stock levels observed in the 1950s be regained by reducing fishing mortality? Projections based on production modeling assume that they can, but if exogenous forces (for example, habitat loss or pollution) have affected the stock, it may be that they cannot. If the recent pattern of lower fishing mortality rates in response to social and economic factors continues, the fishery will in essence conduct an experiment that may answer the question.

Introduction

The purpose of this study is to illustrate areas of uncertainty that have been or are being addressed within the context of Atlantic menhaden stock assessments and to suggest additional areas for future consideration. By “uncertainty,” we mean imprecision or bias in data, model choice, and estimation methods, as well as in the resulting assessment results, specifically in benchmarks used for management. Much of the information contained in this paper is provided annually to the Atlantic Menhaden Advisory Committee (AMAC) of the Atlantic States Marine Fisheries Commission.

Natural history and exploitation

Atlantic menhaden *Brevoortia tyrannus* is a euryhaline clupeid found in coastal and intertidal waters from West Palm Beach, Florida, to Nova Scotia, Canada (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 summer; older and larger fish are generally found farther north. Southward migration begins in early fall, with surface schools last seen in late December or early January off the Carolinas. Spawning occurs principally at

sea, from May to October off southern New England and the mid-Atlantic states and from October to April off the southeastern United States. Eggs hatch at sea and larvae are moved into estuaries by ocean currents (Nelson et al. 1977), where they metamorphose into juveniles. In late fall and early winter, juveniles leave the estuaries and move into large bays or open waters. Adult menhaden are filter feeders feeding primarily on phytoplankton and, in turn, support predatory fishes and sea birds.

Sampling of juvenile Atlantic menhaden by the National Marine Fisheries Service began in 1955. In the 1970s, sampling activities culminated in extensive coastwide trawl surveys, conducted through 1978 (Ahrenholz et al. 1989). A stream survey (two streams each in North Carolina and Virginia) was continued through 1986. Ahrenholz et al. (1989) found no significant correlations between relative juvenile abundance estimates and later fishery-dependent estimates of year-class strength. However, recent investigation with state data sets (described later) have shown more promise (Vaughan and Smith 1999), but more work is needed to better separate a small number of age-1+ menhaden from juveniles (age-0).

As noted in Ahrenholz et al. (1987), fishing on Atlantic menhaden has occurred since colonial times, but the purse seine fishery for reduction began in New England about 1850. Landings and nominal

effort (measured as number of weeks a vessel unloaded during the fishing year, vessel-weeks) are available since 1940 (Figure 1). Landings rose during the 1940s (from 167,000 to 376,000 t), peaking during the 1950s (high of 712,000 t in 1956), and then declined during the 1960s (from 576,000 t in 1961 to 162,000 t in 1969). During the 1970s the stock rebuilt (landings rose from 250,000 t in 1971 to 376,000 t in 1979), and then maintained intermediate levels during the 1980s (varying between 238,000 t in 1986 when fish meal prices were extremely low to 418,600 t in 1983). Landings during the 1990s have varied between 245,900 t in 1998 and 401,200 t in 1990. Through analysis of extensive catch-effort data bases, Clark and Mangel (1979) demonstrated that catchability is frequently density dependent and thus catch per unit effort (CPUE) and nominal fishing effort are poor measures of population abundance and fishing mortality rate in purse seine fisheries. Schaff (1979) demonstrated density-dependent catchability in the Atlantic menhaden stock, with a statistical relationship that fits remarkably well ($R^2 = 0.77$).

The number of fish reduction plants, the main users of the resource, has declined from more than twenty during the late 1950s to two in 2000; one

in Reedville, Virginia, and one in Beaufort, North Carolina. Similarly, the number of purse-seine vessels in the reduction fishery has declined from more than one hundred thirty vessels during the late 1950s to twelve during 2000.

Assessment and management

Annual estimation of six “trigger” variables is required by the Atlantic menhaden fishery management plan [Atlantic Menhaden Advisory Committee (AMAC) 1992] (Table 1). These variables were developed by the AMAC for evaluation of the health of the Atlantic menhaden stock (AMAC 1992). The first three variables are estimated directly from fishery statistics: (1) reported landings in weight from the reduction fishery, (2) proportion of age-0 Atlantic menhaden in the landings by number, and (3) proportion of adult (age-3+) Atlantic menhaden in the landings by number. Three remaining trigger variables are obtained from virtual population analysis (VPA), and have less precision associated with current year estimates. These variables include (4) recruitment to age 1 in numbers, (5) spawning stock biomass (weight of mature females in metric tons estimated

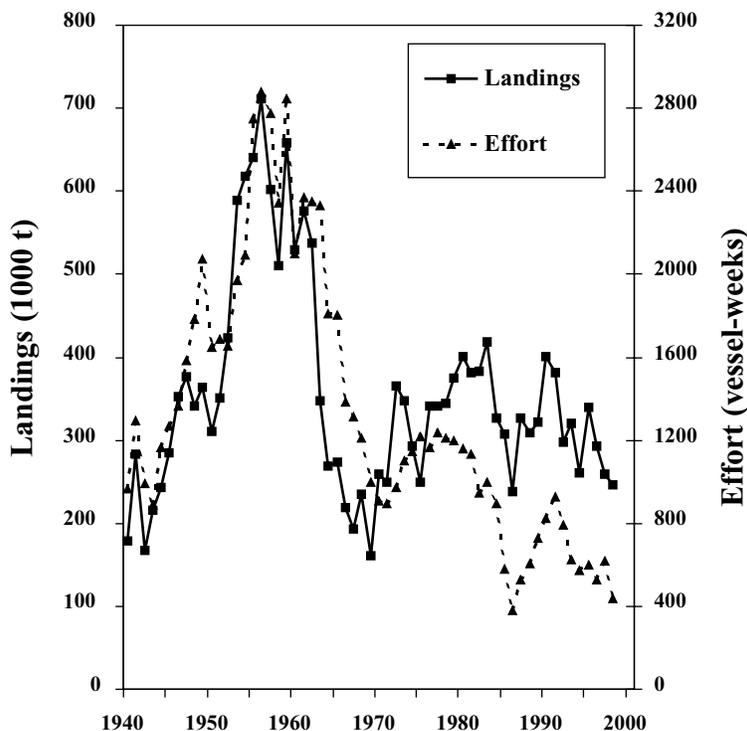


FIGURE 1. Atlantic menhaden landings and nominal fishing effort (vessel-weeks).

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TABLE 1. Annual estimated values of six Atlantic menhaden triggers. (Boldface indicates years in which respective trigger would have been exceeded.)

Year	Landings ^a	P0 ^b	P3+ ^c	Recruitment ^d	SSB ^e	SPR ^f
1940	179.0	-	-	-	-	-
1941	283.1	-	-	-	-	-
1942	167.4	-	-	-	-	-
1943	215.0	-	-	-	-	-
1944	243.5	-	-	-	-	-
1945	285.6	-	-	-	-	-
1946	351.8	-	-	-	-	-
1947	376.4	-	-	-	-	-
1948	341.3	-	-	-	-	-
1949	363.4	-	-	-	-	-
1950	311.2	-	-	-	-	-
1951	351.3	-	-	-	-	-
1952	423.6	-	-	-	-	-
1953	589.2	-	-	-	-	-
1954	617.9	-	-	-	-	-
1955	641.4	24.4	20.1	3.1	327.0	13.8
1956	712.1	1.0	15.5	5.7	258.7	6.6
1957	602.8	8.5	7.1	7.3	133.2	6.7
1958	510.0	3.9	4.4	3.3	88.7	16.1
1959	659.1	0.2	8.4	15.1	173.7	8.6
1960	529.8	2.6	7.7	2.2	123.3	24.1
1961	575.9	0.0	48.6	3.0	360.3	13.3
1962	537.7	2.5	33.3	2.2	200.0	4.9
1963	346.9	5.5	13.3	2.2	65.3	3.1
1964	269.2	17.5	6.8	1.7	30.8	2.4
1965	273.4	17.1	6.2	1.9	20.8	1.7
1966	219.6	26.1	2.7	1.4	9.1	3.3
1967	193.5	0.7	8.0	1.9	20.9	5.5
1968	234.8	13.4	6.7	1.2	16.8	2.1
1969	161.6	18.2	6.2	1.7	14.1	5.4
1970	259.4	1.5	2.6	2.6	16.2	6.6
1971	250.3	7.5	11.2	1.3	28.1	6.6
1972	365.9	2.9	11.3	3.4	48.0	2.0
1973	346.9	3.0	2.5	2.7	12.5	1.3
1974	292.2	15.9	2.6	3.0	12.1	1.5
1975	250.2	13.8	2.6	3.7	13.6	1.9
1976	340.5	8.4	1.7	6.8	15.6	2.8
1977	341.1	13.2	2.8	5.1	25.6	4.3
1978	344.1	14.8	9.5	4.7	44.5	3.7
1979	375.7	38.6	3.9	4.2	40.4	6.4
1980	401.5	2.6	9.2	6.7	58.0	4.6
1981	381.3	29.8	7.2	4.7	42.4	5.0
1982	382.4	3.6	12.7	6.4	48.8	3.1
1983	418.6	24.5	4.2	2.5	35.8	3.8
1984	326.3	36.5	9.5	3.8	55.3	1.7
1985	306.7	21.1	2.9	5.0	18.8	2.5
1986	238.0	5.1	3.5	4.5	15.7	7.5
1987	327.0	1.9	7.8	3.4	37.5	7.8
1988	309.3	15.7	17.6	3.0	58.9	5.1
1989	322.0	5.7	6.4	5.5	38.3	5.2
1990	401.2	14.3	7.6	2.2	35.3	7.7
1991	381.4	27.8	9.6	3.5	59.6	2.8
1992	297.6	19.5	6.3	3.5	29.8	8.6
1993	320.6	4.3	10.3	3.2	39.3	10.1
1994	260.0	5.9	16.1	2.4	62.9	13.0
1995	339.9	3.5	23.2	2.9	74.7	9.5
1996	292.9	3.1	15.6	2.1	54.9	13.9
1997	259.1	2.5	30.0	2.0	102.1	14.0
1998	245.9	7.6	20.5	1.3	73.2	11.5

TABLE 1. (continued)

Year	Landings ^a	P0 ^b	P3+ ^c	Recruitment ^d	SSB ^e	SPR ^f
Median ^g	324.1	13.6	7.1	3.4	26.9	4.1
25%	250.3	3.6	3.7	2.2	15.7	2.1
75%	365.9	18.2	10.3	4.7	42.4	5.5
Trigger	<250.0	>25.0	>25.0	<2.0	<17.0	<3.0

^a Landings in thousands of metric tons.

^b Percent by numbers of age 0's in landings.

^c Percent by numbers of adults (ages 3+) in landings.

^d Estimated numbers of recruitment to age 1 in billions.

^e Estimated mature female biomass (spawning stock biomass or SSB) in thousands of metric tons.

^f Estimated equilibrium maximum spawning potential based on egg production (for estimated F vs $F = 0$) in percent (includes F at age 0).

^g Median, 25th, and 75th percentiles based on fishing years from 1965 through 1990, except for P3+ which is based on fishing years 1955 through 1990.

on March 1), and (6) percent maximum spawning potential (or static spawning potential ratio, static SPR), estimated as the ratio between egg production with and without fishing, under equilibrium conditions. The triggers are considered annually along with other information on stock status to determine the need for management.

Detection of a series of poor year classes was a major concern when the triggers were developed. By the time the first trigger variable (landings) is reduced below the warning level, possibly because of poor recruitment, the recent recruiting year classes to the stock that support the fishery are one or two years in the past. The second trigger variable (proportion of age-0 menhaden in the landings) may be indicative of a good recruit year-class, but in many cases it seems to indicate good weather late in the year instead. The third trigger variable (proportion of adults, age-3+, in the landings) was designed to indicate whether one or more moderate to strong year classes are followed by several weak year classes (poor recruitment). The fourth trigger variable (recruitment to age-1) is a direct estimate of recruitment, and is particularly sensitive to retrospective error. The fifth trigger variable (spawning stock biomass) is indicative of whether there are sufficient spawners available to improve chances for adequate subsequent recruitment, but the weak spawner-recruit relationship for Atlantic menhaden gives no guarantee that moderate to high recruitment will come from high spawning stock (and may suggest the reverse). The sixth trigger variable (% maximum spawning potential) compares an index of egg production by mature females (summed over all mature ages) under equilibrium assumptions and the estimated F to the same index with $F = 0$. Thus, the sixth trigger variable is a

measure of fishing mortality, or the rate at which stock abundance is being reduced annually because of fishing activity, and is not a measure of spawning stock biomass.

Virtual population analysis is used to reconstruct the fish population and fishing mortality rates by age and year, typically assuming a constant rate of natural mortality (M). In most stock assessments, constant values for M are obtained from life history analogies (e.g., maximum age, growth rates), with the methods of Pauly (1979) and Hoenig (1983) among the most widely used. Estimates of M in the early literature on Atlantic menhaden vary, although only moderately (Ahrenholz et al. 1991). Schaaf and Huntsman (1972) estimated $M = 0.37$ /year based on an ad-hoc approach regressing total mortality rate (Z) on fishing effort. Nearly 438,000 juvenile Atlantic menhaden were tagged coastwide, 1970–1986; estimates were $M = 0.52$ /year from a preliminary tag-recovery analysis (Dryfoos et al. 1973), and $M = 0.50$ /year from a more extensive tag-recovery analysis (Reish et al. 1985). The mean of the range ($M = 0.45$ /year) has been used routinely in Atlantic menhaden assessments beginning with Ahrenholz et al. (1987).

Errors in VPA-based quantities are usually greatest in the most recent year analyzed. Estimates for previous years quickly converge to true values, provided that catch at age and natural mortality are well estimated and that fishing mortality is at least moderate (Jones 1961; Tomlinson 1970; Pope 1972, Ulltang 1977; Megrey 1989). Thus, VPAs in successive years often give revised estimates of stock status in what was the final year of a previous VPA. For some stocks, such revised estimates display patterns suggestive of bias (i.e., current-year estimates

consistently appear to have been too high or too low). The susceptibility of an assessment procedure to retrospective errors can be evaluated using *retrospective analysis*, which recreates an historical series of VPAs using a specified assessment procedure (Sinclair et al. 1990). The remaining three trigger variables are subject to this source of potential error.

Analyses that support advice to management contain additional uncertainty from various sources. Such uncertainty in analyses of Atlantic menhaden has been investigated in several contexts, including effects of sampling error (Dorval 1998) and the retrospective problem (Cadrin and Vaughan 1997). Simulation of the population through time has been used to examine alternative management scenarios (Vaughan 1977a, 1993).

Analyses presented in this study build on the above areas of uncertainty. Two general areas of analysis are described. The first area is largely deterministic and encompasses virtual population analysis and related work. Uncertainty associated with development of the catch-at-age matrix (or catch matrix) is briefly discussed. Some discussion and updating of retrospective and historical analyses are presented. Typically natural mortality (M) is assumed to be constant over all ages and years; here, we explore the sensitivity of our analyses to age-varying M . Fishery-independent indices of recruitment (juvenile abundance surveys) that have become available recently are compared with lagged estimates of recruitment to age-1 from the VPA. Although they have not yet proved useful for calibrating VPA, these indices have been helpful in confirming recruitment patterns obtained from VPA.

The second area of analysis includes stochastic projections and an alternative modeling approach, which itself includes a form of stochasticity. Population models such as yield per recruit, spawning stock biomass per recruit, and various stock-recruitment relationships were developed from annual, age-specific estimates of population size and fishing mortality rates. Various biological reference points can be obtained from these modeling approaches (e.g., $F_{0.1}$, F_{max} , and $F_{x\%}$, where $x\%$ represents a specified level of SPR). Population projections under alternate levels of fishing mortality can be made, after assuming a specific relationship between spawning stock and subsequent recruitment. The stock-recruitment relationship is probably the greatest source of uncertainty in any attempted population projection (Vaughan 1977b). The event-tree approach used here is based on conditional

probabilities developed from the historical pattern of recruitment and spawning stock biomass, rather than from an assumed mathematical relationship (Vaughan 1993). Finally, application of different modeling approaches may provide additional insight. Hence, results from an alternative approach based on surplus production models are compared with those from VPA.

Methods

The Beaufort Laboratory (NMFS) has conducted coastwide biological sampling of Atlantic menhaden for length and weight at age since 1955, and the result is one of the longest time series of biological data on an exploited fish stock in the nation. The reduction fishery is sampled for fish size and age according to a two-stage cluster design (first stage consisting of purse-seine sets and second stage consisting of individual fish from each sampled set), conducted over the range of the fishery, both temporally and geographically (Chester 1984). Number of fish sampled in the second cluster was reduced during the early 1970s from 20 fish to 10 fish to increase sampling intensity of the first cluster (number of sets). This sampling program provided the basic data for VPA and subsequent analyses.

Virtual population analysis (VPA)

This section includes analyses conducted on the catch-at-age matrix used by the VPA, output from the VPA, including consideration of retrospective error and comparison of VPA with age-fixed M to those with age-variable M . In addition, VPA estimates of recruitment to age-1 are compared with a coastwide juvenile abundance index developed from state indices covering Florida to southern New England.

Catch-at-age matrix and VPA results.—The catch-at-age matrix was developed on a plant-week basis from detailed landings and biological sampling data. An analysis of internal consistency of this matrix is based on pairwise correlations between lagged catches from a cohort. This approach permits one to assess the ability of the catch matrix to follow a cohort through its lifetime. One should be able to follow a strong cohort (or a weak cohort) from full recruitment (at least age-2) through its eventual disappearance from the stock. However, there is an implicit assumption that F is relatively constant over time, as changes in F could reduce the correlations.

Our VPA methods generally followed those described in Ahrenholz et al. (1987), Vaughan and Smith (1988), Vaughan (1990, 1993), Vaughan and Merriner (1991), and Cadrin and Vaughan (1997). Using the Murphy (1965) VPA approach applied separately to each cohort, annual age-specific estimates of fishing mortality rate (F) and population numbers are obtained. A constant value of M (0.45/year) was used. Starting values for final F for complete cohorts were estimated from the catch curve for the cohort. A separable VPA approach was applied to recent years (1995–1998) in developing starting fishing mortality rates on oldest ages for incomplete cohorts (Clay 1990). Median values with their interquartile range (25th and 75th percentiles) were computed to provide historical perspective on estimates of the last three trigger variables (1955–1998).

A detailed retrospective analysis for Atlantic menhaden is presented in Cadrin and Vaughan (1997) and is not repeated here. The retrospective analysis was accomplished using separable virtual population analysis with catch-at-age data for 1970 through a variable final year (1984–1995). Cadrin and Vaughan (1997) also presented an historical analysis based on the series of trigger reports to AMAC, which is updated in this paper. The estimates in Cadrin and Vaughan (1997) updated here are from the revised Atlantic menhaden fishery management plan (FMP) (AMAC 1992) and annual trigger reports to AMAC (Vaughan 1994–1999). Comparisons are based on proportional error between estimates from the terminal year (1998) with estimates from prior years (1990 and 1992–1997). Proportional error is calculated for prior year estimates by subtracting and then dividing by terminal year estimates.

Age-specific estimates of M .—With very few exceptions, stock assessments routinely assume a constant M across years and ages. Assessments for Atlantic menhaden have followed this approach. However, the usual assumption of constant M over all ages is probably not realistic, especially when young ages (i.e., age 0 and age 1) are included in the analysis. An empirical relationship devised by Boudreau and Dickie (1989) was to be used to obtain annual, age-specific estimates of M as a function of mean weight at age:

$$\hat{M} = 2.88(592W)^{-0.33}, \quad (1)$$

where W is weight (in pounds) at age. Thus, as the fish grows, M declines with age. Assuming decreasing M with increased size (or age) seems biologically reasonable (e.g., Gulland 1987), but this assumption

has not been widely adopted in marine stock assessments. For example, the Boudreau and Dickie (1989) method was used in assessments of Atlantic weakfish *Cynoscion regalis* (Seagraves 1992), but was later rejected by a review committee (SARC 1998). The basis for the SARC (1998) rejection was in specifying the functional relationship of M with age, rather than the concept that M varies (declines) with age. Proportional error is used to present the general magnitude of difference between estimates of recruitment, SSB, and static SPR for the age-variable M and age-fixed M . Proportional error is calculated from the age-variable M estimates by subtracting and then dividing by age-fixed M estimates. The analysis presented here is for the purpose of exploring the sensitivity of our VPA to age-varying estimates of M and the effect on management benchmarks.

Juvenile abundance indices.—Recently, extant data sets of predominantly juvenile menhaden have been made available by states along the U.S. Atlantic coast; including South Carolina (SEAMAP), North Carolina, Virginia, Maryland, Connecticut, and Rhode Island. When averaging indices within or between states, all indices are first standardized by subtracting the series mean and dividing by the series standard deviation.

Menhaden data collected by the SEAMAP program were provided by South Carolina Department of Natural Resources. Trawl sampling was conducted from coastal North Carolina (primarily south of Cape Fear River) to northern Florida in 1989–1998 during spring (April–May), summer (June–August), and fall (September–October). Standardized indices are calculated for each season and averaged across seasons for each year to form a SEAMAP juvenile abundance index (1989–1998).

Four juvenile indices were provided by the North Carolina Division of Marine Fisheries: (1) Alosid seine index (1972–1998), (2) Albemarle striped bass nursery trawl index (1982–1998), (3) Pamlico Sound survey index (1987–1998), and (4) NC juvenile trawl survey index (1987–1998). These indices were standardized and averaged across the four indices by year to form a North Carolina juvenile abundance index (1972–1998).

Juvenile Atlantic menhaden CPUE for 1959–1998 was obtained from annual striped bass seine surveys conducted by the Maryland Department of Natural Resources. Indices of Atlantic menhaden abundance were computed, based on arithmetic means for each of the four main regions (head

of the Chesapeake Bay and the Choptank, Nanticoke, and Potomac rivers) from the Maryland survey. Standardized indices for each region were calculated, and then averaged across the four regions. A similar index of juvenile Atlantic menhaden for tributaries to the Virginia portion of Chesapeake Bay (1980–1998) was provided by the Virginia Institute of Marine Sciences (VIMS) based on samples from the lower portion of rivers where Atlantic menhaden are found. Standardized Maryland and Virginia indices were averaged to form a Chesapeake Bay juvenile abundance index (1959–1998).

Juvenile Atlantic menhaden indices were also obtained from the Connecticut Department of Environmental Protection (indices from fall 1984–1998 trawl survey and from 1987 to 1998 Connecticut River alosid survey) and from the Rhode Island Department of Fish and Wildlife (indices from 1990 to 1998 juvenile finfish survey of Narragansett Bay and 1979–1998 trawl survey of Rhode Island coastal waters). Each index was first standardized and then averaged to form statewide Connecticut and Rhode Island indices. These, in turn, were again standardized and averaged to form a southern New England juvenile abundance index (1979–1998).

A coastwide juvenile abundance index (1972–1998) was developed as a weighted average of standardized indices for SEAMAP (weight = 0.15), North Carolina (weight = 0.35), Chesapeake Bay (weight = 0.45), and southern New England (weight = 0.05). Statistical weights by regions are based on estimates of relative juvenile menhaden density \times area¹. Only North Carolina and Chesapeake Bay indices were combined for 1972–1978, southern New England was included for 1979–1988, and all four regions were included for 1989–1998.

Stochastic projections and alternate approach

In this section, we develop biological reference points that serve as the basis for subsequent event tree simulated projections. An alternative approach based on surplus production models is also considered.

Biological reference points for projections.—Yield per recruit and spawning stock biomass per recruit (static SPR) were estimated based on partial recruitment for 1995–1998, using the numerical yield-per-recruit (YPR) approach of Ricker (1975).

¹by Dr. D. Ahrenholz, NOAA Center for Coastal Fisheries and Habitat Research, Beaufort, North Carolina (personal communication)

Unlike the analytical approach of Beverton and Holt (1957), which assumes knife-edged recruitment to the fishery, Ricker's approach allows for partial recruitment at ages not fully recruited (e.g., ages 0 and 1 compared with age 2). Static SPR (the sixth trigger variable used for Atlantic menhaden) compares spawning stock biomass per recruit calculated for different levels of fishing mortality to spawning stock biomass per recruit calculated with $F = 0$ under an equilibrium (static) assumption (Gabriel et al. 1989; Mace et al. 1996). Thus, the comparison is not to "virgin" spawning stock biomass, but to a theoretical spawning stock biomass under the assumption that life history parameters are not affected by fishing. Benchmark values of instantaneous fishing mortality rates (F) were developed from yield per recruit ($F_{0.1}$ and F_{max}) and from static spawning potential ratio (F_{10} and F_{20}) approaches for Atlantic menhaden.

Event tree projections of recruitment and SSB.—Event-tree techniques were used to replace the usual functional stock–recruit model with an empirically derived probabilistic model of recruitment conditioned on spawning stock biomass or other measure of spawning capacity. Simulations were made consisting of 25-year population projections (replicated 100 times) using the event tree approach described in Vaughan (1993) as the only source of uncertainty. To define the event tree, conditional probabilities of recruitment to age 0 given spawning stock biomass were estimated from historical estimates of spawning stock biomass and subsequent recruitments to age 0, as estimated by VPA for 1955–1998. A set of 100 replicates of 25-year projections was accomplished for each level of fishing mortality (described below). In these projections natural mortality ($M = 0.45/\text{year}$) was assumed constant. The estimated population age structure for 1997 (from VPA) was used as the initial age structure for projections. Parameters from annual von Bertalanffy growth equations and fitted weight-length equations, averaged for 1995–1998 (the most recent four-year period), were used to represent growth. Output of particular interest from these simulations are recruitment to age 1 and spawning stock biomass (trigger variables 4 and 5 represented in Figure 2A and B).

Current fishing mortality was obtained from the mean estimates of age-specific F for the period 1995–1998 (when only Virginia and North Carolina plants have been active in the reduction fishery) from the most recent Murphy VPA. Mean age-specific F forms the basis of partial recruitment (relative mortality at age) used for varying estimates

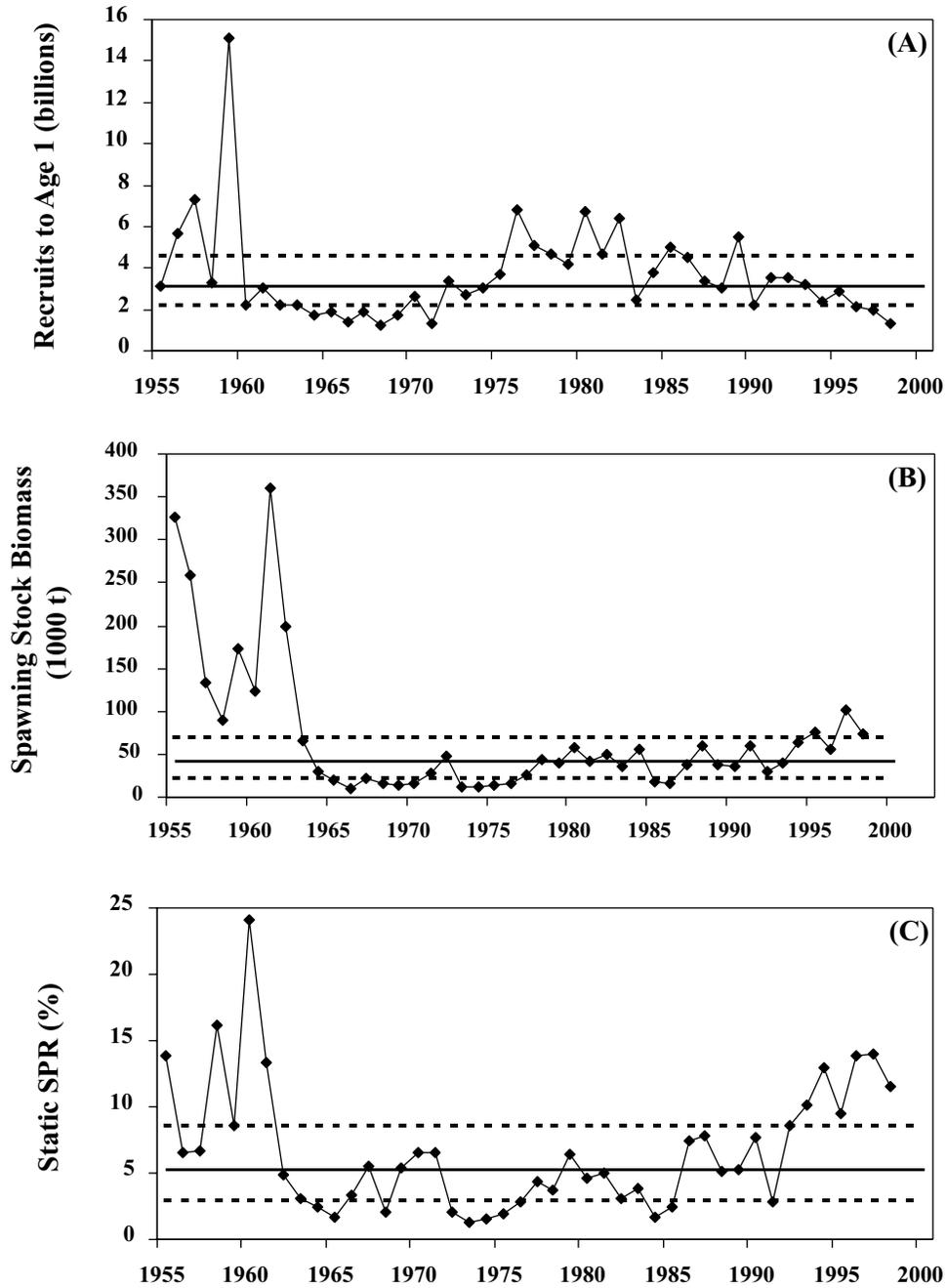


FIGURE 2. Historical plots for (A) recruitment to age-1 (R_1), (B) spawning stock biomass (SSB), and (C) static spawning potential ratio (SPR) for Atlantic menhaden with their temporal median and interquartile range.

of age-specific F according to the biological reference points developed from yield per recruit and spawning stock biomass per recruit analyses. Projections are then based on the fishing mortality associated with two biological reference points obtained from yield-per-recruit analysis ($F_{0.1}$ and F_{\max}), from static spawning potential ratio analysis (F_{10} and F_{20}), and from F_{rep} . The reference point F_{rep} is based on spawning stock biomass per recruit, uses the median of plotted R/SSB, and compares the inverse (median SSB/R) to the theoretical curve of SSB/R (values in Figure 2C are proportional to SSB/R) (Sissenwine and Shepherd 1987). Because estimates of F form the basis of the projections and the final trigger variable (static SPR) is calculated directly from F , there would be no uncertainty associated with this variable. Hence, output from these projections include only the first five trigger variables.

Surplus production models.—Surplus production modeling was used in addition to VPA to obtain an additional perspective on population dynamics. In this, we used data on total annual landings in weight. Annual data on either relative abundance or relative fishing mortality rate were also required; we used estimates of stock biomass (ages 0+) derived from the VPA. Biomass was used rather than recorded data on fishing effort rate because our production model assumed constant catchability q , and density-dependent catchability has been demonstrated in this species (Schaaf 1979). Using biomass estimates also allowed us to set $q = 1$, thus reducing the number of estimated parameters by one.

Production models assume that the stock's production of new biomass B per unit time t is a function solely of current stock biomass; that is,

$$\frac{dB}{dt} = f(B) \quad (2)$$

Under this fundamental assumption, biomass can be removed from the stock at this same rate dB/dt while leaving the stock size unchanged; thus the time rate of production as given above is often denoted surplus production, equilibrium yield, or sustainable yield.

The simplest, logistic form of production model was described by Lotka (1924) as a model of population growth; Schaefer (1954, 1957) applied it to fisheries problems, while adding a term for fishing mortality; Pella (1967) showed how to fit the model without assuming that observed yields are equilibrium yields; and Prager (1994) introduced several refinements, including the use of bootstrapping to estimate nonparametric confidence intervals. Under

the logistic model, the production function is a parabola, which implies that the curve of production as a function of biomass is symmetrical. Using the parameterization of Fletcher (1978),

$$\frac{dB_t}{dt} = 4m \frac{B_t}{K} - 4m \left(\frac{B_t}{K} \right)^2, \quad (3)$$

where B_t is stock biomass at time t , m is maximum sustainable yield, and K is the maximum population size, or carrying capacity, of the stock. In the Pella-Tomlinson generalized production model (Pella and Tomlinson 1969), the production curve could be skewed in either direction. In the improved parameterization of Fletcher (1978),

$$\frac{dB_t}{dt} = 4g \frac{B_t}{K} - 4g \left(\frac{B_t}{K} \right)^n, \quad (4)$$

where n is a parameter determining the shape of the production function, and g (used for notational convenience) is the following function of n :

$$g = \frac{n^{n/n-1}}{n-1}. \quad (5)$$

It appears that few data sets on real populations provide enough information to obtain useful estimates of n in equation (4) (Hilborn and Walters 1992).

In fitting, we used an observation-error estimator, conditioned on the observed yield and estimated in logarithmic transformation, as implemented by an extended version of the ASPIC computer program (Prager 1995). We fit both logistic and generalized production models and made projections based on model results and several assumed levels of future landings.

Results

Virtual population analysis

Catch-at-age matrix and VPA results.—Coherence of the catch matrix is presented in Table 2. Significant correlations ($P < 0.05$) were obtained for all lagged catches through age 6, with the exception of nonsignificant correlation between catches at age 2 with age 6 four years later ($P = 0.165$). Although this does not imply that the catch matrix is without error, it does suggest an exceptionally high degree of precision to the catch matrix.

Estimates of the last three triggers for 1955–1998, derived from the most recent assessment (Vaughan and Smith 1999), are summarized in Table 3. Estimates of historical recruitment to age-1 range between 1.2 billion in 1968 and 15.1 billion

TABLE 2. Coherence of Atlantic menhaden catch-at-age matrix based on pair-wise correlations of subsequent catches from each cohort, 1955–1998. For each age, the Pearson correlation coefficient is shown in the first row, and the probability of exceeding this coefficient under the null hypothesis that the coefficient equals zero is in the second row.

Age	1	2	3	4	5	6
1	1.0 0.0	0.59 0.0001	0.77 0.0001	0.80 0.0001	0.76 0.0001	0.37 0.0222
2	–	1.0 0.0	0.55 0.0001	0.47 0.0016	0.53 0.0003	0.22 0.1652
3	–	–	1.0 0.0	0.92 0.0001	0.71 0.0001	0.37 0.0166
4	–	–	–	1.0 0.0	0.75 0.0001	0.58 0.0001
5	–	–	–	–	1.0 0.0	0.83 0.0001

in 1959 (1958 cohort). The estimate for the most recent year (1998) is 1.3 billion. The historical median is 3.1 billion, and the interquartile range is between 2.2 and 4.6 billion. Historical estimates of spawning stock biomass have ranged between 9,100 t in 1966 and 360,300 t in 1961 (when the 1958 cohort was 3 years of age). The estimate for the most recent year is 73,200 t in 1998. The historical median is 41,400 t and the interquartile range is between 20,900 t and 69,300. Similarly, historical estimates of static SPR have ranged between 1.3 in 1973 and 26.0 in 1960 (when the 1958 cohort became fully recruited to the

fishery). The estimate for the most recent year is 11.5% in 1998. The historical median is 5.3% and the interquartile range is between 2.9% and 8.6%. The historical period covered by this catch-at-age matrix includes a period when the stock was extremely large (during the late 1950s), a period when it was seriously depressed (1960s and early 1970s), and one when it apparently had recovered (late 1970s and 1980s). In recent years, there has been declining recruitment, increasing spawning stock biomass, and historically high values for static spawning potential ratio (reduced fishing mortality).

TABLE 3. Current estimates of VPA-generated indices (“triggers”) and juvenile abundance indices, compared to their long-term median and quartiles. Estimates for 1998 that fall within the interquartile range are not considered markedly different from the long-term median.

Variable	n	Current estimate (1998)	25th pctl	Historical median estimate	75th pctl
Population-Based (VPA) Triggers:					
Fixed M:					
R ₁ (billions)	44	1.3	2.2	3.1	4.6
SSB (1000 t)	44	73.2	20.9	41.4	69.3
SPR (%)	44	11.5	2.9	5.3	8.6
Variable M:					
R ₁ (billions)	44	4.6	2.5	3.4	5.0
SSB (1000 t)	44	65.5	19.9	37.9	62.1
SPR (%)	44	10.1	2.2	4.0	6.3
Standardized Juvenile Abundance Indices for:					
SEAMAP	10	1.36	–0.98	–0.08	1.23
NC Combined	27	0.33	–0.80	–0.10	0.46
VA Seine	19	–0.77	–0.74	–0.35	0.44
MD Seine	40	–0.87	–0.94	–0.32	0.83
CT Combined	15	0.73	–0.59	–0.31	0.23
RI Combined	20	1.68	–0.39	–0.39	–0.37
Coastwide	27	0.02	–0.43	0.13	0.64

Historical and retrospective analysis of the Atlantic menhaden VPA revealed substantial inconsistency in estimates of management variables in the last year of stock assessments (Cadrin and Vaughan 1997). Retrospective error of management variables in terminal years was positively skewed but not biased. Cadrin and Vaughan (1997) found that historical estimates of management variables converged to similar values within three years. An updated historical analysis using proportional error based on Murphy VPA runs is summarized for the VPA-based triggers (Figure 3), to show recent performance of current estimates of these trigger values. As a cohort appears in the landings for more years, its year-class strength is better estimated. Initial estimate of recruitment to age 1 is based directly on fishing mortality estimated by separable VPA on some recent short time period (this process is used for incomplete cohorts). Once the cohort is represented by age 4 or age 5 in the catch matrix, little if any change in recruitment to age 1 occurs, because uncertainty in starting (final) F converges quickly for Atlantic menhaden. Recently, initial estimates of recruitment to age 1 for a given cohort have been low (often below the trigger warning level of 2 billion). As the cohort is fished for additional years, progressively increasing estimates of recruitment have been more commonly obtained.

Age-specific estimates of M .—Sensitivity of VPA-based output was explored using the Boudreau and Dickie (1989) approach of equation (1), yielding estimates of M averaged across 1955–1998 as follows: age 0, $M = 0.82/\text{year}$; age 1, $M = 0.58/\text{year}$; age 2, $M = 0.46/\text{year}$; and age 3 and older, $M = 0.34/\text{year}$. The estimate of M averaged over all ages (0–8) and all years was 0.46, similar to the constant M of 0.45/year that has been used historically in Atlantic menhaden VPAs. The VPA-based triggers for 1955–1998 were re-estimated with age-specific M . Estimates of recruitment to age 1 ranged from 1.3 billion in 1968 to 16.3 billion in 1959 (1958 cohort). Proportional error suggests slightly higher estimates of recruitment to age-1 were obtained with age-variable M compared with age-fixed M (Table 3; Figure 4). However, estimated recruitment in 1998 is much higher, relative to the estimate based on age-fixed M .

Historical estimates of spawning stock biomass range between 8,400 t in 1966 and 325,000 t in 1961 (when the 1958 cohort was 3 years of age). The estimate for the most recent year is 65,500 t in 1998. The historical median is 37,900 t and the interquartile

range is between 19,900 t and 62,100 t. Generally lower estimates of spawning stock biomass were obtained with age-variable M compared with age-fixed M . Similarly, historical estimates of static SPR range from 1.0 in 1973 to 19.2 in 1960 (when the 1958 cohort became fully recruited to the fishery). Based on variable M , static SPR for Atlantic menhaden has never been above 20% including a period of very robust stock size. The estimate for the most recent year is 10.1% in 1998. The historical median is 4.0% and the interquartile range is between 2.2% and 6.3%. Generally lower estimates of spawning stock biomass were obtained with age-variable M than with age-fixed M . Again, this information suggests that in recent years there has been declining recruitment (though with apparent increase in 1998), increasing spawning stock biomass, and historically high values of static spawning potential ratio (i.e., reduced fishing mortality).

Juvenile abundance indices.—There was limited consistency among the juvenile abundance indices by region that were combined to create the coastwide index (Table 4). The SEAMAP index was marginally correlated ($P < 0.1$) with the Chesapeake Bay combined juvenile abundance index (VA and MD). The North Carolina and New England indices were uncorrelated with each other as well as with the other regional indices. As might be expected, the SEAMAP, North Carolina and Chesapeake Bay juvenile abundance indices were all highly correlated with the Coastwide index ($P < 0.01$). The southern New England indices, which had minimal (5%) contribution to the coastwide index, was uncorrelated with the coastwide index. There were highly significant pairwise correlations found for MD–VA and CT–RI. Finally, the coastwide and Chesapeake Bay juvenile abundance indices were highly correlated ($P < 0.01$) with estimates of lagged recruitment (Figure 5).

The most recent values of these juvenile abundance indices are compared with their median and interquartile range (Table 3). Only the Virginia seine index is below its 25th percentile. The Maryland seine and coastwide indices fall between the 25th percentile and median. The North Carolina combined index falls between the median and 75th percentile. The SEAMAP, Connecticut combined, and Rhode Island combined indices all fall above the 75th percentile of their historical time series. We suggest that the interquartile range is an appropriate measure of historical performance against which to compare recent performance. Hence, values outside the

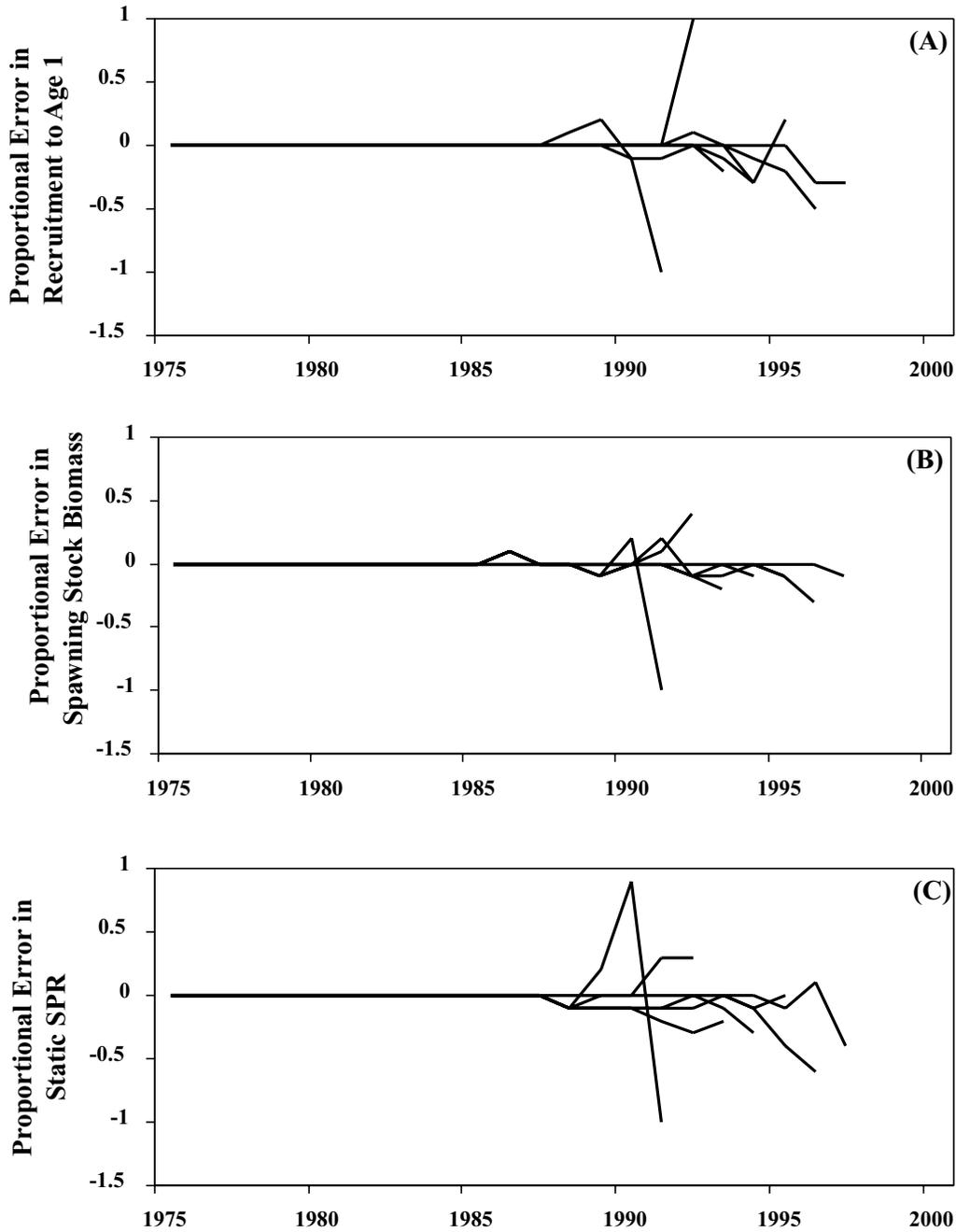


FIGURE 3. Retrospective error expressed as proportional error relative to the terminal year for (A) recruitment to age 1 (R_1), (B) spawning stock biomass (SSB), and (C) static spawning potential ratio (SPR) for Atlantic menhaden.

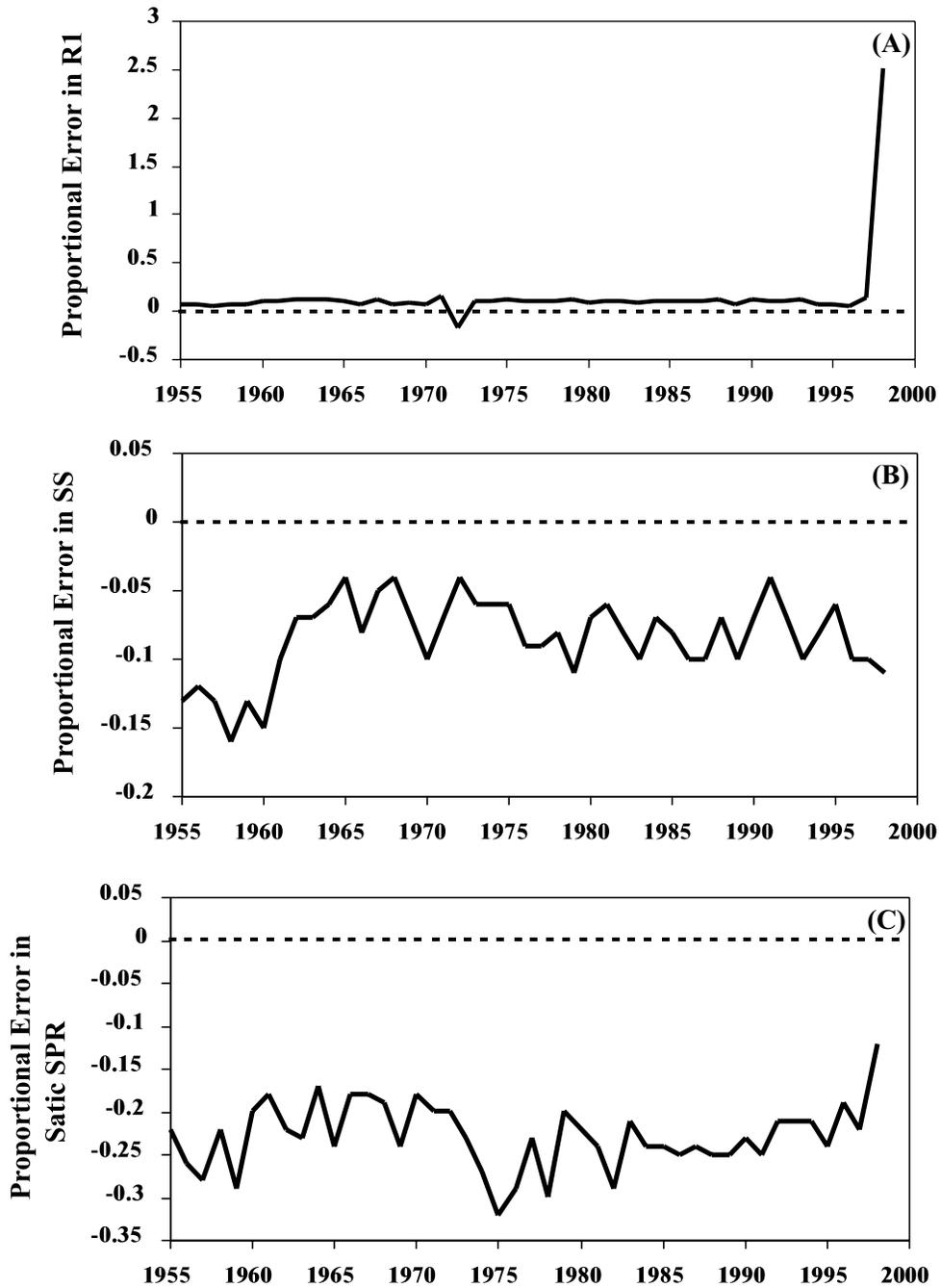


FIGURE 4. Sensitivity of virtual population analysis (VPA) based on age-variable M expressed as proportional error relative to VPA analysis based on age-fixed M for (A) recruitment to age 1 (R_1), (B) spawning stock biomass (SSB), and (C) static spawning potential ratio (SPR) for Atlantic menhaden.

TABLE 4. Coherence among regional juvenile abundance indices and with lagged recruits to age 1. For each index, the Pearson correlation coefficient is shown in the first row, the probability of exceeding this coefficient under the null hypothesis that the coefficient equals zero is in the second row, and sample size in the third row. Regions represented are U.S. south Atlantic bight (SEAMAP), North Carolina (NC), Chesapeake Bay (CB), southern New England (NE), and coastwide (Coast). Significant values ($P < 0.1$) indicated by asterisk, highly significant values ($P < 0.01$) indicated by double asterisk.

Index	SEAMAP	NC	CB	NE	Coast	Lagged R ₁
SEAMAP	1.0	0.51	0.59*	0.04	0.80**	0.38
	0.0	0.1334	0.0719	0.9089	0.0051	0.3111
	10.0	10.0	10.0	10.0	10.0	9.0
NC	–	1.0	0.24	0.31	0.75**	0.23
		0.0	0.2205	0.1841	0.0001	0.2529
		27.0	27.0	20.0	27.0	26.0
CB	–	–	1.0	–0.33	0.82**	0.68**
			0.0	0.1490	0.0001	0.0001
			27.0	20.0	27.0	26.0
NE	–	–	–	1.0	–0.11	–0.10
				0.0	0.6573	0.6902
				20.0	20.0	19.0
Coast	–	–	–	–	1.0	0.58**
					0.0	0.0019
					27.0	26.0

interquartile range can be interpreted as low or high relative to their historical performance, while values within the interquartile range cannot be interpreted as different from the median value.

Stochastic projections, production models

Biological reference points for projections.— Current F is given by the vector ($F_0 = 0.02$, $F_1 = 0.21$, $F_{2+} = 0.95$) based on selectivity for the reference period of 1995–1998. The biological reference points described below were estimated based on the same selectivity of F on ages 0 and 1 relative to age 2 and older (ages at full F). Biological reference points traditionally obtained from the yield-per-recruit approach include F_{max} and $F_{0.1}$ (Figure 6). The reference point F_{max} represents the level of fishing mortality that in theory maximizes biomass return to the fishery, and $F_{0.1}$ is a modification of F_{max} based on an economic-return argument. The reference point $F_{0.1}$ is that level of F that occurs where the slope of the curve of yield-per-recruit versus F is 10% of its slope at the origin. This reference point was proposed as providing nearly the same yield in biomass as F_{max} , but with less expenditure of fishing effort and less chance of overfishing (Gulland and Boerema 1973). For Atlantic menhaden, F_{max} occurs at a full F (mean F over ages 2–8) of about 1.0, while $F_{0.1}$ occurs at a full F of about 0.5. Biological reference points

based on static SPR are given as F subscripted with the level desired for static SPR (Figure 6). Hence, F_{20} refers to the level of F that would produce a theoretical ratio of 20% SPR. The reference point F_{20} occurs at full F of about 0.7, and F_{10} at about 1.1. In calculating F_{rep} , we obtained the median SSB/R for the historical Atlantic menhaden data (12.4 expressed as 1,000 t per million recruitment). The corresponding F from the SSB/R curve generated for the partial recruitment during 1995–1998 was interpolated at 0.9 (F_{rep}).

Event tree projections of recruitment and SSB.— Conditional probability diagrams were developed that relate the historical pattern in recruitment to age 0 or age 1 given the spawning stock biomass (SSB) that produced them (Table 5). Low, moderate and high are based on the interquartile range of the historical time series for SSB and recruitment (as in Vaughan 1993). The historical pattern of recruitment to age 1 (1956–1998) conditioned on SSB (1955–1997) suggests that low SSB (below the 25th percentile) has about a 36% chance of producing low recruitment, a 45% chance of producing a moderate recruitment, and only 18% chance of producing high recruitment. Thus, there is a tendency towards low recruitment when SSB is low (i.e., SSB < 20,900 t). Probabilities of recruitment to age-1 also were obtained for moderate and high SSB. Moderate SSB is somewhat more likely to produce high

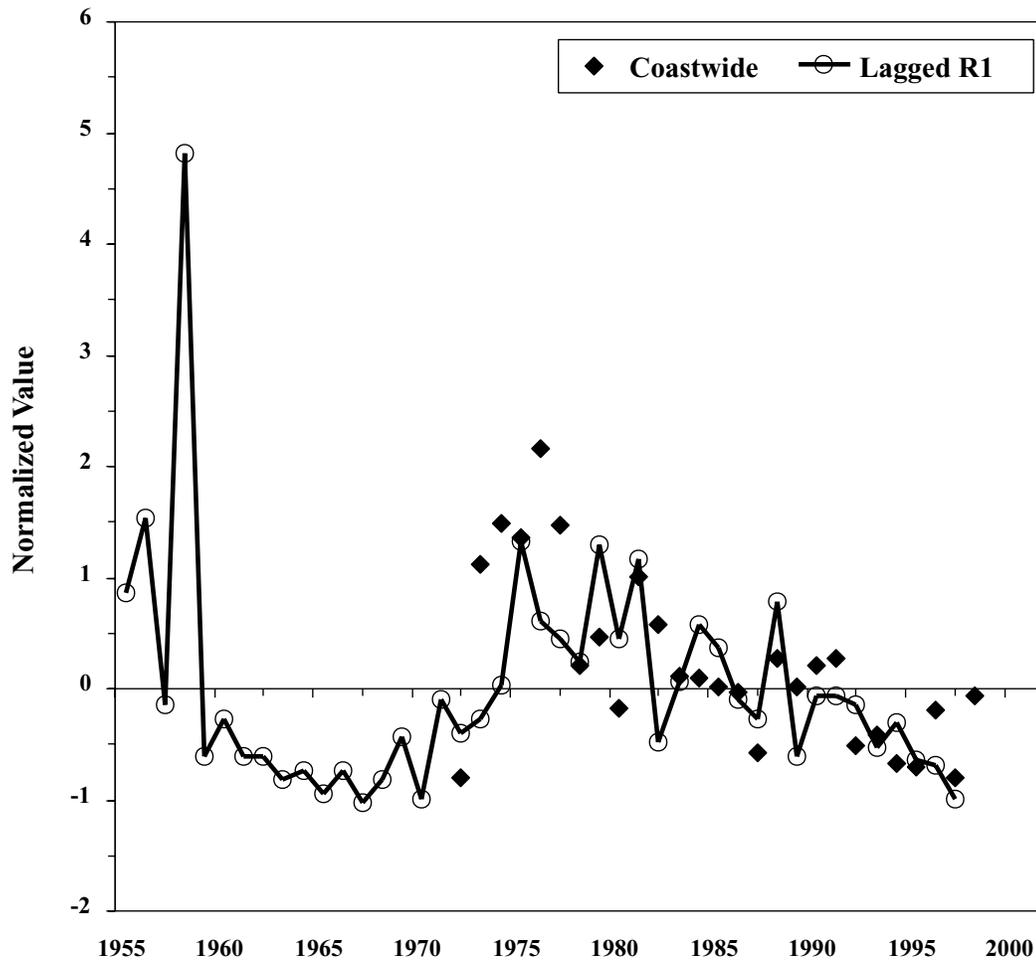


FIGURE 5. Comparison of coastal juvenile abundance index with lagged recruitment to age-1 (R_1) for Atlantic menhaden.

recruitment (23%) than low recruitment (27%); while high SSB is as likely to produce low (30%) as high recruitment (30%). This analysis suggests that maintaining SSB above approximately the 25th percentile for the long-term data series (20,900 t) will give a higher probability of good recruitment.

The conditional probabilities of recruitment to age-0 given SSB were used in the population projections to relate current spawning stock to subsequent recruitment (Vaughan 1993) (Table 5). Annual survival at age in these projections were based on constant M and age-specific F for the biological reference points developed from yield per recruit and spawning stock biomass per recruit analyses. Because static SPR is directly related to F , static SPR was not simulated in these projections. The 25-year

projections are replicated 100 times with underlying error (estimated from historical data). The annual median and interquartile range of the fourth and fifth trigger variables are plotted for the event tree simulation approach (Figures 7–11). The results of these projections are for comparison only and are not intended as predictions of future values. The projections suggest no significant difference in recruitment to age-1 whether fishing at $F_{0.1}$ ($F = 0.5$) or F_{10} ($F = 1.1$). On the other hand, spawning stock biomass is expected to be higher when fishing at $F_{0.1}$ ($F = 0.5$) compared with F_{10} ($F = 1.1$).

The cumulative probability (or risk) of decline in recruitment to age 1 is developed from the 100 replicates of the projections in their 10th year (2007) (Figure 12). Risk is defined as the cumulative

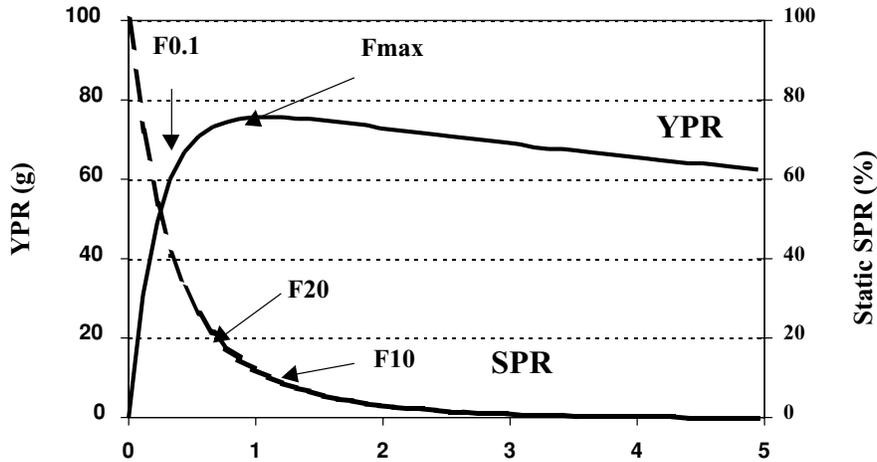


FIGURE 6. Critical values of instantaneous fishing mortality rates (F) from yield per recruit ($F_{0.1}$ and F_{max}) and from static spawning potential ratio (F_{10} and F_{20}) for Atlantic menhaden. The estimate of present F is for an age-at-entry of 0.5 years and mean and partial recruitment based on 1995–1998.

probability of a value less than or equal to a given value of recruitment. Considerable overlap exists among the curves associated with each of the biological reference points. Furthermore, all risk curves shown suggest moderate probability of falling below the current warning level of this trigger variable (2 billion age-1 recruits). These values range from

30% from F_{max} to 39% for F_{rep} and F_{20} , with intermediate values of 36% and 37% for $F_{0.1}$ and F_{10} , respectively.

Similarly, the cumulative probability (or risk) of decline in spawning stock biomass (SSB) is developed from the 100 replicate projections in their 10th year (2007) (Figure 13). Risk is defined as

TABLE 5. Conditional probabilities of recruitment to age 0 and to age 1 from spawning stock biomass stratified by interquartile range for 1955–1998. Conditional probabilities for recruitment to age 0 from spawning stock biomass used in population projections. Recruitment to age 0 and age 1 are in billions and spawning stock biomass is in thousands of metric tons (t).

Recruitment to:	Spawning stock biomass		
	Low (<20.9)	Moderate (20.9–69.2)	High (>69.2)
	Age 0		
Low (<2.79)	0.273	0.182	0.300
Moderate (2.79–6.12)	0.454	0.591	0.400
High (>6.12)	0.273	0.227	0.300
	Age 1		
Low (<2.22)	0.364	0.227	0.300
Moderate (2.22–4.57)	0.454	0.500	0.400
High (>4.57)	0.182	0.273	0.300

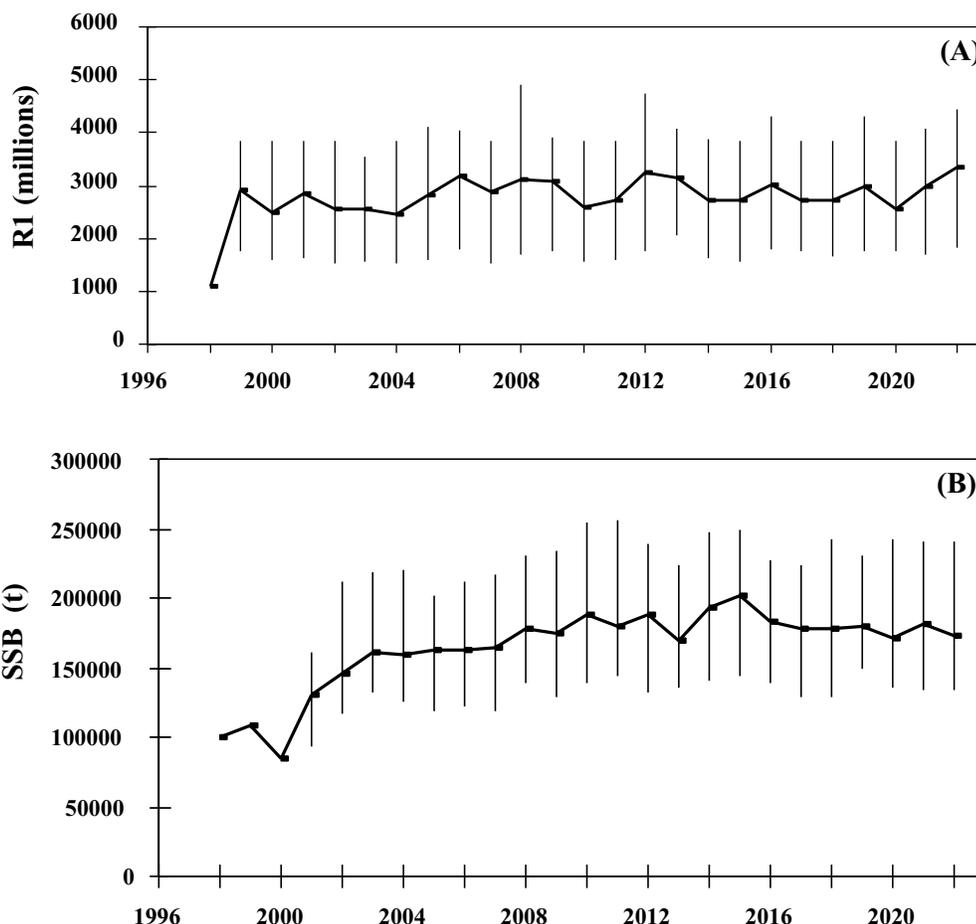


FIGURE 7. Projected values for $F = 0.5$ ($F_{0.1}$) of (A) recruitment to age 1, and (B) spawning stock biomass of Atlantic menhaden (interquartile range displayed).

the cumulative probability of a value less than or equal to a given value of SSB. SSB associated with lower values of F give lower risk of being below a specified value of SSB. That is, the probability of falling below 40,000 t, varies between 0% from for $F_{0.1}$, F_{20} , and F_{rep} , and 11% for F_{10} , with an intermediate value for F_{max} (6%). However, all risk curves shown exhibit only a minuscule probability of falling below the current warning level of this trigger variable (17,000 t).

We also examined the statistical properties of recruitment of Atlantic menhaden (to age 1) for different ranges of spawning stock biomass (Table 6). In addition to mean values, nonparametric statistics are calculated that are less sensitive to nonnormal (highly skewed) distribution of R_1 attributable to the remarkable strength of the 1958 year-class. These statistics include the median (or 50th percentile) and

the 25th and 75th percentiles. The interquartile range, defined by the 25th and 75th percentiles, is a nonparametric analog to the standard deviation. Although the mean value of R_1 trends upward with increasing minimum spawning stock biomass, this is a result of the reduced sample size and the increasing effect of the recruitment to age 1 in 1959 (1958 year-class). It does not demonstrate increased likelihood of improved recruitment. No trend is evident in the median value (the lowest median value shown is for SSB values in excess of the 75th percentile of the historical time series for SSB). There is some indication of improvement in the upper limit of the interquartile range (75th percentile) with increasing spawning stock biomass at or above its historic median level (41,400 t).

Surplus-production models.—Results of fitting logistic and generalized models were quite similar;

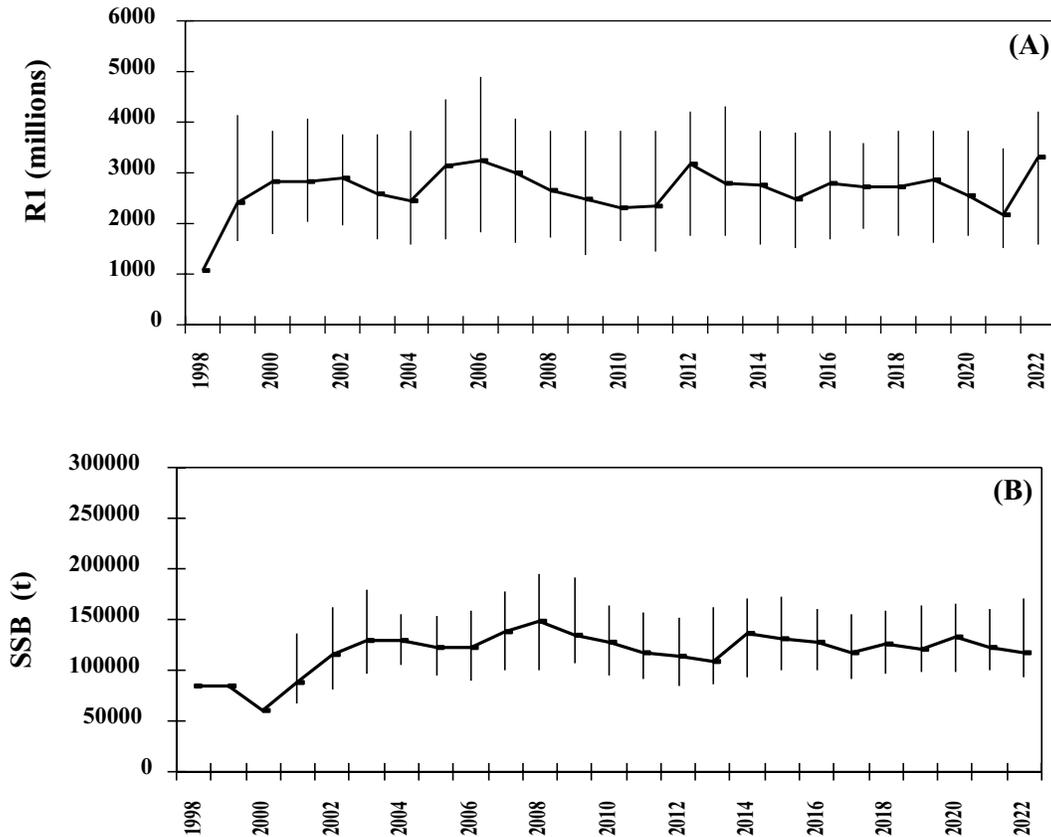


FIGURE 8. Projected values for $F = 0.7$ (F_{20}) of (A) recruitment to age-1, and (B) spawning stock biomass of Atlantic menhaden (interquartile range displayed).

here, we report primarily on the logistic model. This model fit the data reasonably well (Figure 14A); fit of the generalized model was quite similar. The largest discrepancies between observed and estimated CPUEs are in the years of peak abundance centered around 1960, where the production model, perhaps because it lacks age structure, is unable to replicate rapid changes in stock size. Estimates of benchmarks (Table 7) seem reasonable given the history of the stock. Estimated time trajectories of biomass and fishing mortality rate relative to their respective benchmarks B_{MSY} and F_{MSY} depict a stock that has been below the benchmark B_{MSY} since about 1960, and fishing mortality rate that has been above F_{MSY} for most of the time period (Figure 14B).

The generalized production model estimated that MSY was slightly larger than the logistic model and about the same stock status (Table 7). The shape exponent of the generalized model was estimated as $n = 2.76$, which skews the curve to the left so that $B_{MSY} = 0.81 K$ (whereas in the logistic model,

$B_{MSY} = 0.5 K$). As the generalized model with its free exponent is more complex than the logistic, an F -ratio test was performed testing $H_0: n = 2$ against the alternative $H_a: n \neq 2$. The test failed to reject H_0 ($P = 0.44$), suggesting the logistic model as a better choice for this stock. We note that the usefulness of the F -ratio test in this context has not been studied.

Projections under constant-catch scenarios estimate that, if the level of yield recorded in 1999 (Figure 15B) or estimated for 2000 (Figure 15C) is taken in 1999–2003, stock biomass will increase to greater than B_{MSY} . If the yield recorded in 1998 is taken, stock biomass will recover, but not to B_{MSY} by 2003. Estimates of fishing mortality rate from the same projections indicate that F will drop below F_{MSY} under all three scenarios. Nonparametric 80% confidence intervals on B and F are extremely narrow, and we emphasize that they include only one source of uncertainty, namely lack of fit of the logistic model to the observed data, which include VPA biomass estimates. To assess the reasonableness of

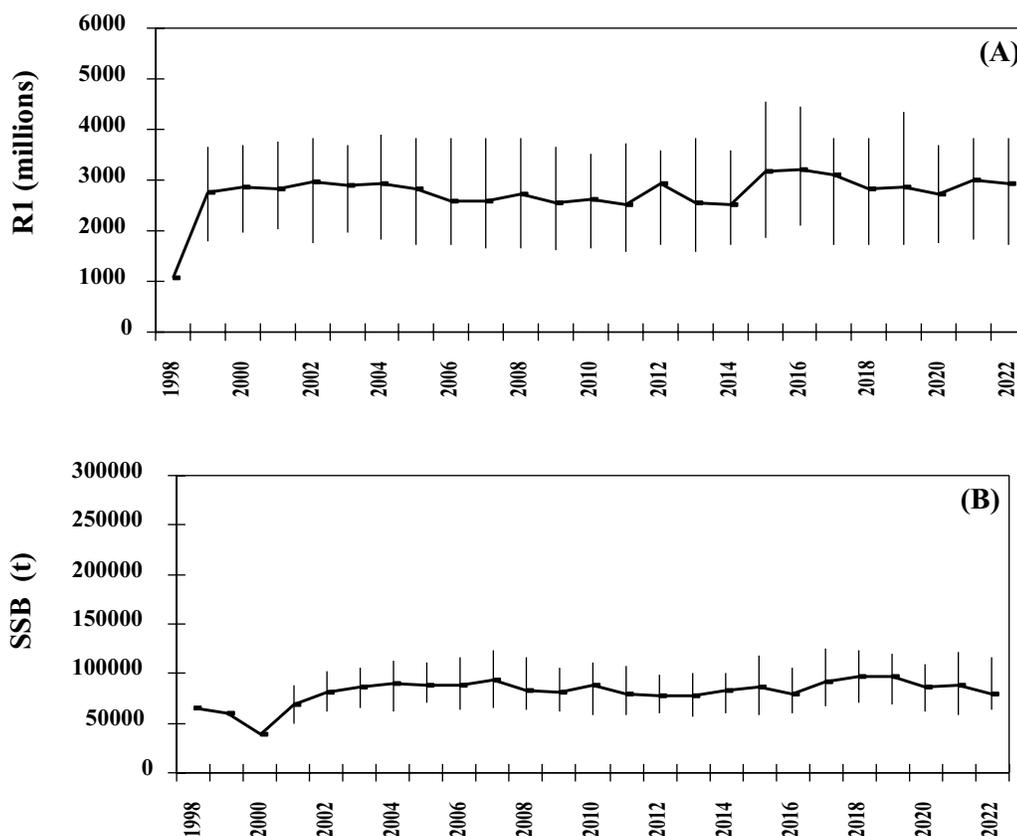


FIGURE 9. Projected values for $F = 0.9$ ($F_{current}, F_{rep}$) of (A) recruitment to age 1, and (B) spawning stock biomass of Atlantic menhaden (interquartile range displayed).

the assumption $q = 1.0$, we refit the logistic model, estimating q ; the resulting estimate was $q = 1.02$, which suggests that the assumption conflicts with neither the data nor the model.

Discussion

Age-structured models

The quality of the catch matrix for the reduction fishery on the Atlantic menhaden is one of the best in the United States. This is partly because of the relatively few reduction plants (especially in recent years), and also because a statistically sound sampling program has been in place for over 40 years. The catch matrix is remarkably consistent and follows cohorts well through time. However, there are several areas where improvement will be needed. The growing bait fishery for menhaden along the Atlantic coast is a source of additional fishing mortality that should be better characterized. Preliminary assessments including bait landings have been

made (Vaughan and Smith 1998). Another source of mortality is bycatch in the shrimp trawl fishery. Because of the poor quality of data available, little has been done to quantify this source of mortality, but the evidence so far suggests that it is minimal.

Occasional criticism has been leveled at the application of untuned virtual population analysis. When applied to poor quality catch matrices, such criticisms are justified. Because of the historic lack of appropriate abundance indices, tuned VPAs have not been applied to menhaden. Attempts to tune VPAs to recently obtained juvenile abundance indices have not been successful to date (Vaughan and Smith 1998, 1999), as model convergence was not achieved. However, this avenue continues to be explored. Regardless, we believe the quality of the Atlantic menhaden catch matrix permits reasonable confidence in the output variables. Because the Atlantic menhaden database is one of the longest in the United States (and the longest in the southeast), these variables can be viewed with reasonable

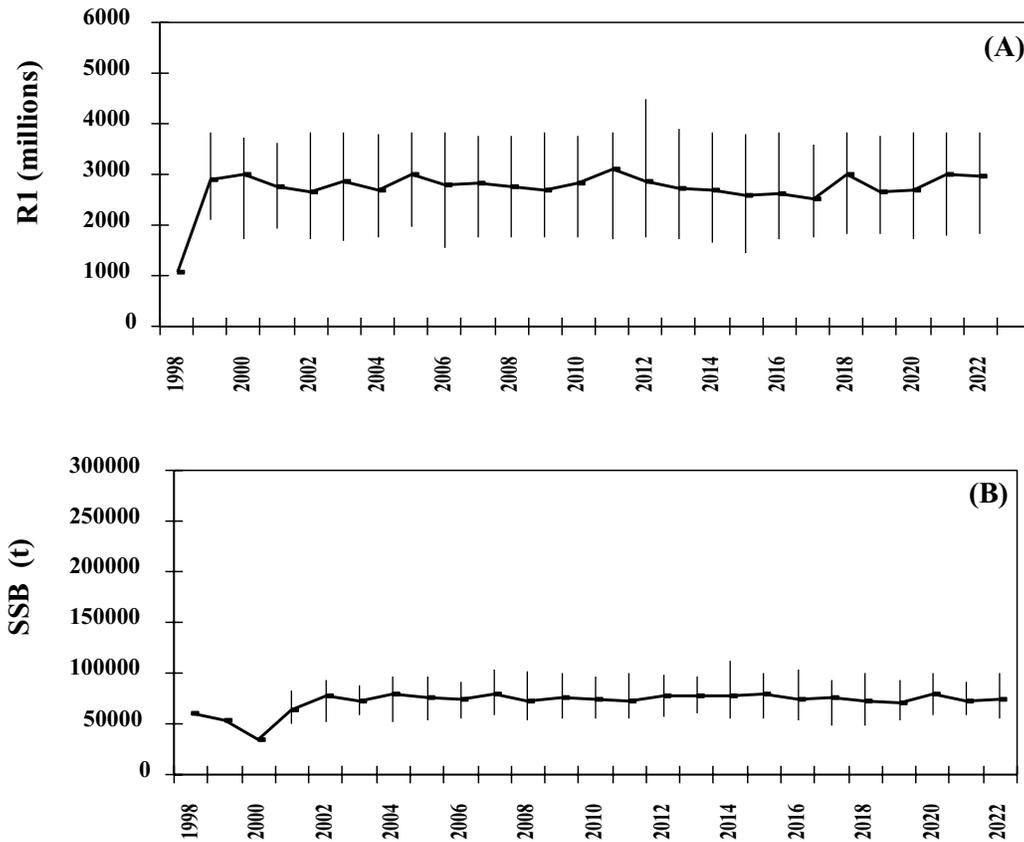


FIGURE 10. Projected values for $F = 1.0$ (F_{max}) of (A) recruitment to age 1, and (B) spawning stock biomass of Atlantic menhaden (interquartile range displayed).

historical perspective. Hence, comparison of recent estimates to the median and interquartile range allows reasonable judgments as to current status of these variables. Thus, recent recruitment is probably low, while recent SSB and static SPR are probably high relative to these historical criteria. The only difference in these historic perspectives when a variable-aged M is used concerns recruitment in the most recent year. This latter approach suggests a recent higher value for recruitment in 1998. Confidence in estimates, especially recruitment, is lacking in the most recent few years, as suggested in Cadrin and Vaughan (1997), and updated historical analyses. Recent estimates of recruitment have been low initially, but have increased for the same year-class in subsequent assessments.

The recently developed coastwide juvenile abundance index compares favorably with our estimates of lagged recruitment to age 1. The level of agreement between the coastwide index and lagged recruits to age 1 serves as support for both

the potential usefulness as a juvenile abundance index, but also supports the validity of the VPA-estimates of recruitment of Atlantic menhaden to age 1. The oldest values of this index are from the Maryland seine index. In more recent years, data from SEAMAP (U.S. South Atlantic Bight), North Carolina, Virginia, Connecticut, and Rhode Island have contributed to this coastwide index. Recent index values, when compared with their respective interquartile range, suggest low values of juvenile abundance from Chesapeake Bay, with moderate to high values outside of this region (Table 3).

A range of biological reference points is presented, based on YPR and static SPR analyses. These reference points form the basis of projections to investigate their utility as specified fishing mortality for management. Very little gain in recruitment to age 1 is suggested by these projections (Figure 12), while significant gains in SSB are evident with decreasing fishing mortality (Figure 13). However, the range of projected spawning stock biomass is consistently

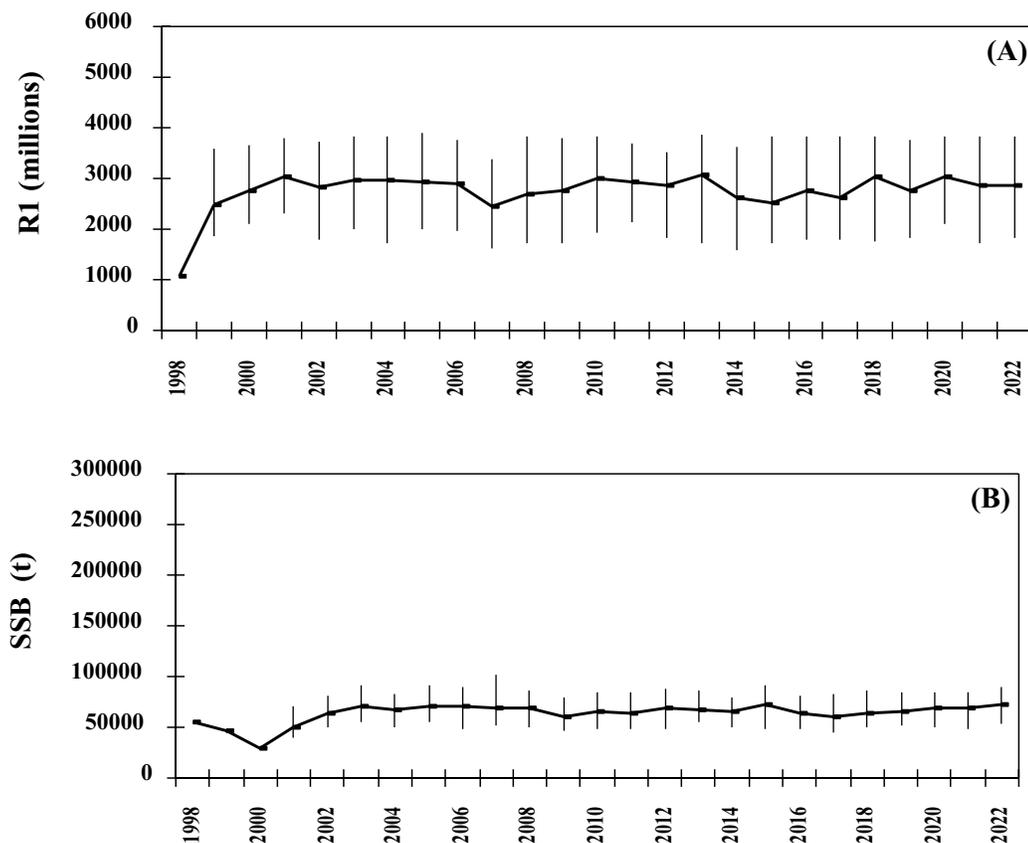


FIGURE 11. Projected values for $F = 1.1$ (F_{10}) of (A) recruitment to age 1, and (B) spawning stock biomass of Atlantic menhaden (interquartile range displayed).

above the current warning level for spawning stock biomass (17,000 t) or above the 25th percentile for the historic period (20,900 t) for all of the biological reference points for F . Furthermore, Myers et al. (1994) have suggested using the expected biomass that would produce half the maximum recruitment from a spawner-recruit relationship as a biological reference point for spawning stock biomass. The Ricker curve for Atlantic menhaden suggests that a spawning stock biomass of 25,300 t produces half the theoretical maximum recruitment to age 1 (2.6 billion). Although the Ricker spawner-recruit curve explains little of the underlying variability observed between recruitment to age 1 and spawning stock biomass, we do not intend to imply that there is no spawner-recruit relationships. If we apply the approach of Myers and Barrowman (1996), we would pose the following three questions: 1) did the greatest recruitment occur when SSB was high (yes, the 1958 cohort was produced when SSB was 89,000 t, the 82nd percentile); 2) did the lowest recruitment occur

when SSB was low (yes, the 1967 cohort was produced when SSB was 21,000 t, the 27th percentile); and 3) was recruitment greater when SSB was above the median than when SSB was below the median (yes, 4.1 billion when above, 3.1 billion when below). Hence, conserving SSB should be a management concern.

Given the high variability in recruitment to age 1 at all levels of SSB, levels of recruitment are similar over the range of fishing mortalities that were simulated. This conclusion is further supported by the analysis on recruitment conditioned on different ranges of SSB (Table 6). These analyses suggest that only “improving” environmental conditions can **assure** improved recruitment. However, as noted earlier, there appears to be some real benefit to recruitment to age-1 from maintaining SSB above about the 25th percentile of its historic range (20,900 t). One caution should be noted. The risk curves themselves have associated uncertainty which has not been formally investigated in this study, although previous

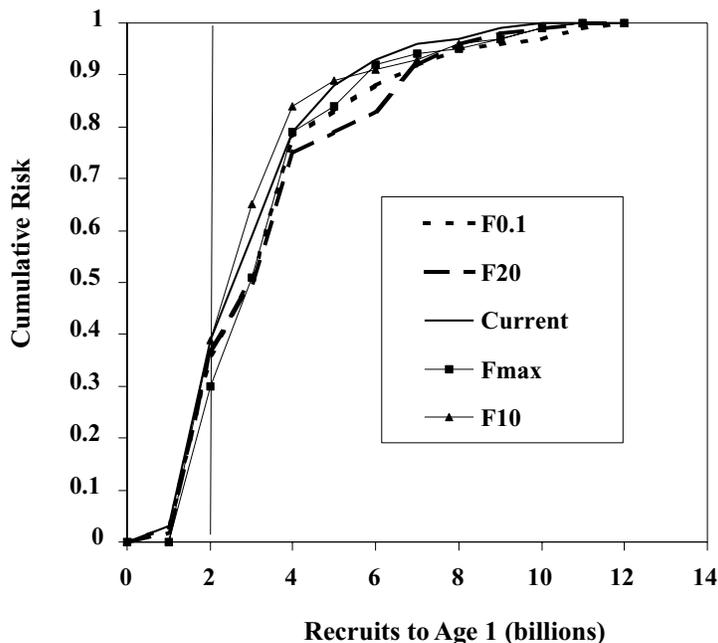


FIGURE 12. Cumulative probability (or risk) of decline in Atlantic menhaden recruitment to age 1 in 2007 for the event tree relationships with projection instantaneous fishing mortality rates based on 5 biological reference points ($F_{0.1}$, F_{max} , F_{10} , F_{20} , F_{rep}). The vertical line represents a “trigger value” (2.0 billion fish) used in management.

experience (Vaughan 1993) would suggest this is relatively small.

Surplus-production models

Production-model estimates depict a stock that has been heavily exploited, perhaps excessively so, since at least the 1960s. As those estimates are made under the rather sweeping assumptions of production modeling, they should be considered together with other information on the stock. Nonetheless, they are consistent with the observations of an earlier study (Schaaf 1979), which held that as early as the mid-1950s, “the harvesting rate exceeded the growth rate of the population.” If in future years fishing mortality is diminished, as in the projections (Figure 15, Figure 16), the population might again attain the levels of the 1950s. However, the projections implicitly assume that fishing mortality and density dependence are the only significant determinants of population size. Whether or not that is the case will in large part determine whether a reduction in fishing mortality will indeed result in those large population sizes.

Uncertainty is understated in most fisheries modeling contexts for several reasons: the variance

of real-world processes appears to be increasing (Steele and Henderson 1984); our data sets are usually quite short; most fishery models are more or less misspecified. The last point is particularly true of the simplest models, such as production models. Uncertainty in production modeling was addressed here through bootstrapping, fitting two model formulations, and verifying the reasonableness of the assumption $q = 1.0$. Bootstrapping provided estimates of confidence intervals on benchmarks and other quantities; examining the generalized model provided insight into uncertainty related to model specification. Nonetheless, estimated confidence intervals in Figure 15 and Figure 16 are probably optimistic, in part because the input “data” include biomass estimates derived from VPA. In such quantities, some of the inherent variability in raw data are lost.

Comparison of approaches

Comparison of VPA and production modeling is comparison of dissimilar things. Virtual population analysis is a more detailed and precise approach, while production models are usually simpler and require less from the user. A more fundamental

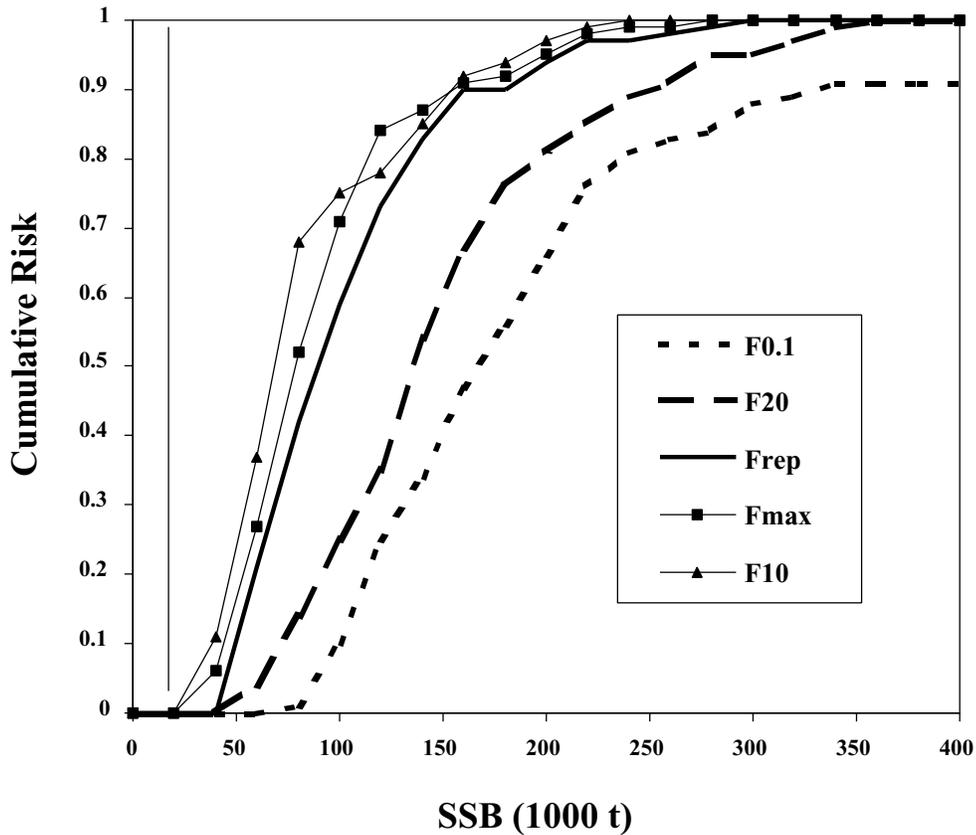


FIGURE 13. Cumulative probability (or risk) of decline in Atlantic menhaden stock biomass in 2007 for the event tree relationships with projection instantaneous fishing mortality rates based on 5 biological reference points ($F_{0.1}$, F_{max} , F_{10} , F_{20} , F_{rep}). The vertical line represents a “trigger value” (17,000 t) used in management.

difference between the two models is that a production model includes an implicit recruitment function, while a VPA does not. Because of this distinction, benchmarks involving sustainability and optimality (e.g., MSY) can be estimated directly from a production model, while VPA estimates must be combined with auxiliary information or models to estimate such benchmarks. Each assessment tool is valuable and provides its own view of the data; neither can be judged “better” than the other.

In the context of the Atlantic menhaden assessment, the two modeling approaches are linked and complementary. They are linked because the input data for production modeling were in fact estimates from VPA. They are complementary because, as mentioned above, the two types of model are useful in estimating different quantities. Here, VPA was used to estimate population quantities; the production model to estimate maximum

sustainable yield and stock status relative to optimal values.

A limited comparison of models can be made by considering what each says about the current state of the stock. The production model estimates that stock biomass is substantially below B_{MSY} , the level that can produce maximum sustainable yield (Figure 14B, Table 7). This reflects a close model fit to biomass estimates (ages 0+) from the VPA (Figure 14A), which indicate that the stock has long been below the remarkably high levels of the 1950s. The production model, however, says nothing specifically about the spawning component of the stock, which the VPA estimates as at high levels in the last few years analyzed (Table 1).

Comparison of estimated fishing mortality rates is more difficult. The production model estimates that the current fishing mortality rate is about 20% higher than the level that could produce MSY (Figure 14B, Table 7). Direct VPA estimates are

TABLE 6. Statistical properties of recruitment to age-1 Atlantic menhaden (R_1 , in billions) dependent on the spawning stock biomass (SSB, t) that produced them.

Range of SSB (t)	Recruitment to age-1 (billions)				
	n	Mean	Median	Percentiles	
				25th	75th
All	44	3.6	3.1	2.2	4.6
Greater than:					
5,300 ^a	44	3.6	3.1	2.2	4.6
17,000 ^b	34	3.7	3.1	2.2	4.7
20,850 ^c	32	3.8	3.1	2.2	4.7
25,300 ^d	31	3.9	3.2	2.2	4.7
41,400 ^e	21	4.1	3.0	2.2	5.0
69,250 ^f	10	4.4	2.6	2.2	5.7
88,000 ^g	9	4.7	3.0	2.2	5.7
Less than:					
5,300	—	—	—	—	—
17,000	10	3.3	3.1	1.9	3.7
20,850	12	3.2	3.1	1.8	4.1
25,300	13	3.1	3.0	1.7	3.7
41,400	23	3.2	3.1	1.9	3.8
69,250	34	3.4	3.1	2.2	4.5
88,000	35	3.4	3.1	1.9	4.5

^a SSB that produces one-half maximum R_1 (Beverton-Holt)
^b Current warning level for spawning stock biomass (SSB)
^c Twenty-fifth percentile for historical SSB (1955–98)
^d SSB that produces one-half maximum R_1 (Ricker).
^e Median SSB for period 1955–98.
^f Seventy-fifth percentile for historical SSB (1955–98)
^g Minimum SSB during 1955–62 (period of historically high levels of SSB).

not compared with any measure of optimality, but it seems that static SPR is currently at relatively high levels (Table 3). The question of stock status, again, depends on whether the high levels of the 1950s can be taken as indicators of what might be possible now. The production model assumes that they can, while an approach based solely on observed percentiles, as in Table 3, tends to discount them as unusual events.

Summary on uncertainty

In our analyses of Atlantic menhaden, we considered uncertainty in a variety of areas, ranging from purely biological to purely statistical, with most uncertainties somewhere in between. Analyses were conducted under alternative assumptions on the natural mortality rate M , one of the most difficult parameters to estimate precisely in any stock assessment. The standard assumption, M invariant with age, is used in most fisheries work; the alternative assumption considered here, M decreasing with age but having the same average value, is probably more

realistic, but has not been widely accepted. We found sensitivity of the assessment to this factor to be minimal.

The retrospective analysis of Cadrin and Vaughan (1997) provides insight into retrospective patterns expected in assessment of this stock by current methods. Unfortunately, understanding of the retrospective problem in general is incomplete; however, the conclusions of Pope (1972) and other investigators are still true: estimates from catch-at-age (VPA) methods are least reliable in the final years. Use of tuning indices has potential to ameliorate this situation somewhat; indices of the Atlantic menhaden stock are in relatively early stages of development.

Event-tree analysis offers a more empirical method of conducting stock simulations than more common methods that use parametric stock-recruitment models. Event-tree projections were used here to examine probable outcomes, in terms of recruitment and spawning-stock size, of various management measures. Simulations using a parametric recruitment model were not reviewed

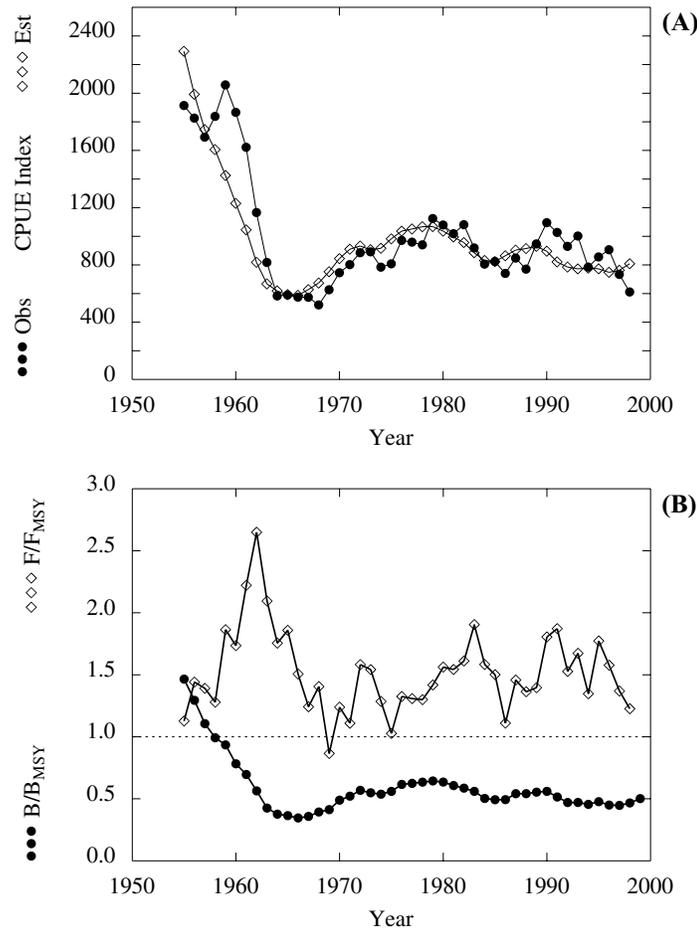


FIGURE 14. Logistic stock-production model of Atlantic menhaden. (A) Observed and estimated CPUE (ages 0+). (B) Estimated time trajectories of age 0+ stock biomass B and annual fishing mortality rate F , each relative to its management benchmark (B_{MSY} and F_{MSY}).

here, but were compared with event-tree analysis by Vaughan (1993).

Use of a production model in addition to the age-structured model (VPA) addresses another area of uncertainty: appropriate model structure. By using both types of model, this assessment examined a wide range of model structure and complexity.

Results of the two types of model were by no means incompatible, but of course the production model depended heavily on VPA results. It may be possible in future assessments to make the methods more independent, perhaps by estimating a density-dependent catchability coefficient within the production model.

TABLE 7. Estimates of three management benchmarks for Atlantic menhaden, estimated by logistic and generalized production modeling. Bias-corrected 80% confidence intervals, derived from bootstrapping, are given for logistic model. For technical reasons, bootstrap was not applied to generalized fit.

Model	MSY (kt/yr)		B_{99}/B_{MSY}		F_{98}/F_{MSY}	
	Point estimate	BC 80% interval	Point estimate	BC 80% interval	Point estimate	BC 80% interval
Logistic	414	391–443	0.50	0.41–0.63	1.23	1.03–1.45
Generalized	433		0.48		1.20	

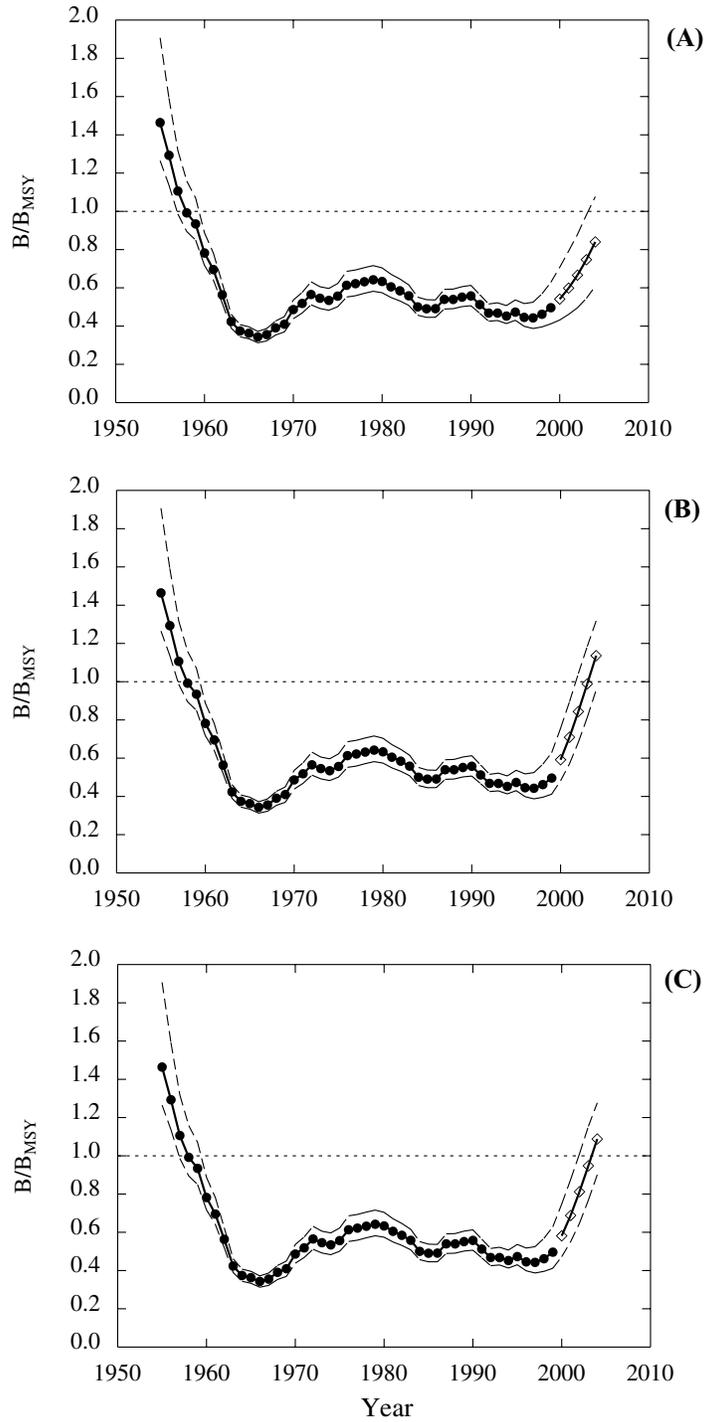


FIGURE 15. Projections of Atlantic menhaden stock based on logistic production-model results. Trajectory of biomass relative to B_{MSY} , assuming yields in 1999–2003 of (A) 245.9 kt/year, the recorded yield in 1998; (B) 171.2 kt/year, the recorded yield in 1999; or (C) 185.0 kt/year, the estimated yield in 2000. Fitted years shown as solid circles; projected years as hollow diamonds; 80% confidence interval as dashed lines.

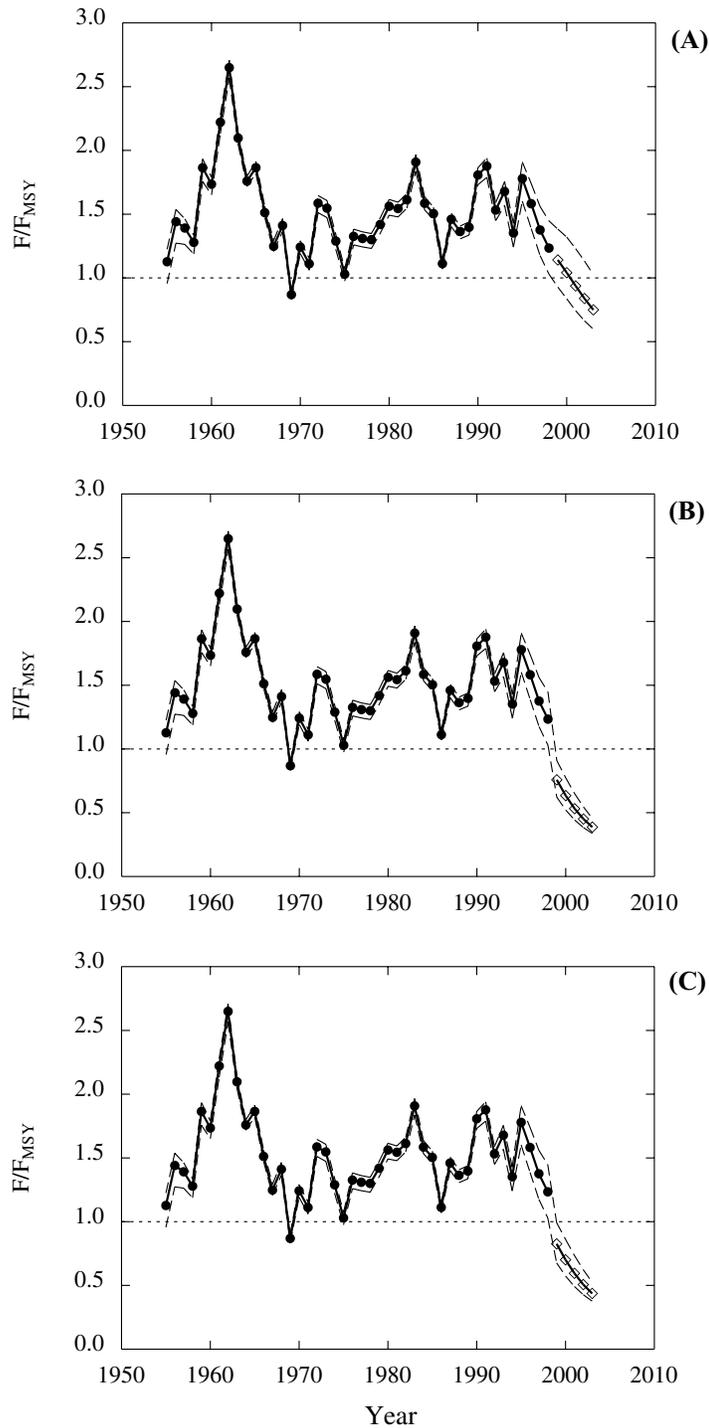


FIGURE 16. Projections of Atlantic menhaden stock based on logistic production-model results. Trajectory of fishing mortality rate relative to F_{MSY} , assuming yields in 1999–2003 of (A) 245.9 kt/year, the recorded yield in 1998; (B) 171.2 kt/year, the recorded yield in 1999; or (C) 185.0 kt/year, the estimated yield in 2000. Fitted years shown as solid circles; projected years as hollow diamonds; 80% confidence interval as dashed lines.

Uncertainties in the production model analysis itself were addressed through both bootstrapping and alternative runs. The bootstrap was used for non-parametric estimates of variability for parameters and related quantities; sensitivity runs were used to examine effects of varying model form, and the validity of the assumption $q = 1.0$. We did not attempt to translate these uncertainties directly into management terms, except to observe that all sensitivity runs estimate essentially the same present stock status.

Projections based on the production model emphasize perhaps the greatest uncertainty about this stock: whether or not the high stock levels of the 1950s can be regained by reducing fishing mortality. If fishing has been the main force regulating the stock size, it should be possible to regain those larger stock sizes with less fishing. However, if external factors—for example, habitat loss or changes in water quality—have contributed markedly to depressing stock sizes, reduced fishing mortality will not result in a remarkably large stock. None of the work here has attempted to answer that question, but if recent reductions in fishing mortality rate and yield continue, an unplanned experiment will take place that may reveal the answer.

Despite the variety of methods used, we believe that uncertainty is routinely underestimated in this and other stock assessments. A variety of assumptions used in modeling serve to reduce apparent uncertainty, yet those assumptions are not entirely valid.

- Autocorrelation is present in most fishery time series; this serves to reduce the information content of the data, and the best method of handling this situation is unclear. In modeling, we tend to assume that this is inconsequential.
- Specification error is the technical term for incorrect formulation of a model. Because all fishery models are highly simplified, specification error always exists. We do not suggest an increase in model complexity, as it is usually accompanied by an increase in variance and can have other undesirable properties, e.g., need for excessive biological data. However, it is important for all concerned to understand that bias from specification error is a likely component of stock assessments.
- Many methods of modeling assume that errors are normally distributed, either in the original data or through transformations. When maximum-

likelihood methods are used for fitting (and many least-squares methods are also maximum-likelihood), model properties are assured only when distributional assumptions are met. Furthermore, some methods of constructing confidence intervals rely on distributional properties. Some results are robust to violations of distributional assumptions, while in other cases, bias or increased variance can result. Only one independent set of estimates is made in each year's assessment, and the effect of high variance can be large errors in those estimates, not just large confidence intervals.

- Finally, fishery scientists universally acknowledge that recruitment depends on unknown environmental factors, yet our lack of knowledge requires us in most cases to model recruitment with little or no environmental influence. The variance of the environment seems to be increasing with time (Steele and Henderson 1984), which can serve to invalidate even previously well-known environmental-biological relationships. This variance in the environment is probably the largest and most poorly understood component of uncertainty in stock assessments, and may elude our grasp indefinitely.

Given all the issues raised here, is stock assessment worthwhile? We believe that it is, provided that it is used together with precautionary principles and with a clear understanding that uncertainty is not just a buzzword, but a consequence of nature. Models will inevitably fail at times, and the measure of any management policy is whether it can succeed in the long term given the profound uncertainties of nature.

Acknowledgments

This work was supported by the U.S. National Oceanic and Atmospheric Administration through the Southeast Fisheries Science Center, NMFS; and the Center for Coastal Fisheries and Habitat Research in Beaufort, North Carolina. We thank D. Ahrenholz, S. Cadrin, J. Waters, and an anonymous reviewer for reviewing the manuscript and for their valuable suggestions.

References

- Ahrenholz, D. W., D. L. Dudley, and E. J. Levi. 1991. Overview of mark-recovery studies on adult and juvenile Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*. Mar. Fish. Rev. 53(4):20–27.

- Ahrenholz, D. W., J. F. Guthrie, and C. W. Krouse. 1989. Results of abundance surveys of juvenile Atlantic and gulf menhaden, *Brevoortia tyrannus* and *B. patronus*. NOAA Technical Report, NMFS 84. Seattle, Washington.
- Ahrenholz, D. W., W. R. Nelson, and S. P. Epperly. 1987. Population and fishery characteristics of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 85:569–600.
- Atlantic Menhaden Advisory Committee (AMAC). 1992. Fishery Management Plan for Atlantic Menhaden, 1992 Revision. Atlantic States Marine Fisheries Commission, Fisheries Management Report 22. Washington, D.C.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Reprinted 1993 by Chapman and Hall, London.
- Boudreau, P. R., and L. M. Dickie. 1989. Biological model of production based on physiological and ecological scaling of body size. Canadian Journal of Fisheries and Aquatic Science 46:614–623.
- Cadrin, S. X., and D. S. Vaughan. 1997. Retrospective analysis of virtual population estimates for Atlantic menhaden stock assessment. Fish. Bull. U.S. 95:445–455.
- Chester, A. J. 1984. Sampling statistics in the Atlantic menhaden fishery. NOAA Technical Report, NMFS 9. Seattle, Washington.
- 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.
- Clay, D. 1990. TUNE: A series of fish stock assessment computer programs written in FORTRAN for microcomputers (MS DOS). Int. Comm. Conserv. Atl. Tunas, Coll. volume Sci. Papers 32:443–460.
- Dorval, E. 1998. Effect of sampling errors on estimates of recruitment and fishing mortality from separable virtual population analysis. Thesis, Old Dominion University, Norfolk, Virginia.
- Dryfoos, R. L., R. P. Cheek, and R. L. Kroger. 1973. Preliminary analyses of Atlantic menhaden, *Brevoortia tyrannus*, migration, population structure, survival and exploitation rates, and availability as indicated from tag returns. Fish. Bull. U.S. 71:719–734.
- Fletcher, R. I. 1978. On the restructuring of the Pella–Tomlinson system. Fish. Bull. U.S. 76:515–521.
- Gabriel, W. L., M. P. Sissenwine, and W. J. Overholtz. 1989. Analysis of spawning stock biomass per recruit: An example for Georges Bank haddock. North American Journal of Fisheries Management 9:383–391.
- Gulland, J. A. 1987. Natural mortality and size. Marine Ecology—Progress Series 39:197–199.
- Gulland, J. A., and L. K. Boerema. 1973. Scientific advice on catch levels. Fish. Bull. U.S. 71: 325–335.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.
- Hoening, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. U.S. 82:898–903.
- Jones, R. 1961. The long term effects of changes in gear selectivity and fishing effort. Mar. Research Dep. Agricul. Fish. Scotland, Ser. 2.
- Lotka, A. J. 1924. Elements of physical biology. Reprinted 1956 as “Elements of mathematical biology.” Dover Press, New York.
- Mace, P. M., D. Gregory, N. Ehrhart, M. Fisher, P. Goodyear, R. Muller, J. Powers, A. Rosenberg, J. Shepherd, and D. Vaughan. 1996. An evaluation of the use of SPR levels as the basis for overfishing definitions in Gulf of Mexico finfish fishery management plans. Report to Gulf of Mexico Fishery Management Council, Tampa, Florida.
- Megrey, B. A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. Pages 8–48 in E. F. Edwards and B. A. Megrey, editors. Mathematical analysis of fish stock dynamics. American Fisheries Society, Symposium 6, Bethesda, Maryland.
- Murphy, G. I. 1965. A solution of the catch equation. J. Fish. Research Board Can. 22:191–201.
- Myers, R. A., and N. J. Barrowman. 1996. Is fish recruitment related to spawner abundance? Fish. Bull. U.S. 94: 707–724.
- Myers, R. A., A. A. Rosenberg, P. M. Mace, N. Barrowman, and V. R. Restrepo. 1994. In search of thresholds for recruitment overfishing. ICES J. March. Sci. 51:191–205.
- 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.
- Pauly, D. 1979. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39:175–192.
- Pella, J. J. 1967. A study of methods to estimate the Schaefer model parameters with special reference to the yellowfin tuna fishery in the eastern tropical Pacific Ocean. dissertation, University of Washington, Seattle.
- Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock production model. Bull. Inter-American Trop. Tuna Comm. 13:419–496.
- Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. N. Atl. Fish. Research Bull. 9:65–74.
- Prager, M. H. 1994. A suite of extensions to a nonequilibrium surplus–production model. Fishery Bulletin, U.S. 92:374–389.
- Prager, M. H. 1995. User’s manual for ASPIC: A stock-production model incorporating covariates, program version 3.6x. NMFS Southeast Fisheries Science Center, Miami Laboratory Document MIA–92/93–55, 4th edition Available from M. H. Prager.
- Reintjes, J. W. 1969. Synopsis of biological data on Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish. Wildl. Serv. Circ. 320.
- Reish, R. L., R. B. Deriso, D. Ruppert, and R. J. Carroll. 1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). Canadian Journal of Fisheries and Aquatic Science 42:1371–1379.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191, 1–382.
- Schaaf, W. E. 1979. An analysis of the dynamic population response of Atlantic menhaden, *Brevoortia tyrannus*, to

- an intensive fishery. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:243–251.
- Schaaf, W. E., and G. R. Huntsman. 1972. Effects of fishing on the Atlantic menhaden stock, 1955–1969. Transactions of the American Fisheries Society 101:290–297.
- Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. Inter-American Trop. Tuna Comm. 1(2):27–56.
- Schaefer, M. B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull. Inter-American Trop. Tuna Comm. 2:247–268.
- Seagraves, R. J. 1992. Weakfish Fishery Management Plan, Amendment #1. Atlantic States Marine Fisheries Commission, Fish. Manage. Rep. No. 20.
- Sinclair, A., D. Gascon, R. O'Boyle, D. Rivard, and S. Gavaris. 1990. Consistency of some northwest Atlantic groundfish stock assessments. North Atl. Fish. Org., SCR Doc. 90/96. Dartmouth, Nova Scotia.
- Sissenwine, M. P., and J. G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Science 44:913–918.
- Smith, J. W., and Population Dynamics Team. 1999. Forecast for the 1999 gulf and Atlantic menhaden purse-seine fisheries and review of the 1998 fishing season. NOAA Beaufort Laboratory, Beaufort, North Carolina.
- Steele, J. H., and E. W. Henderson. 1984. Modeling long-term fluctuations in fish stocks. Science 224:985–987.
- (SARC) Stock Assessment Review Committee. 1998. Consensus Summary of Assessments. 26th Northeast Regional Stock Assessment Workshop (26th SAW), Northeast Fisheries Science Center Ref. Doc. 98-03, Woods Hole, Massachusetts.
- Tomlinson, P. K. 1970. A generalization of the Murphy catch equation. J. Fish. Research Board Can. 27:821–825.
- Ulltang, O. 1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. int. Explor. Mer 37:249–260.
- Vaughan, D. S. 1977a. A stochastic analysis of the stability of the Atlantic menhaden fishery. dissertation, Graduate School of Oceanography, University of Rhode Island, Narragansett.
- Vaughan, D. S. 1977b. Confidence intervals on mortality rates based on the Leslie matrix. Pages 128–150 in W. Van Winkle (editor.), Assessing the Effects of Power-Plant-Induced Mortality on Fish Populations, Pergamon, New York.
- Vaughan, D. S. 1990. Assessment of the status of the Atlantic menhaden stock with reference to internal waters processing. NOAA Tech. Memo. NMFS SEFSC 262. Beaufort, North Carolina.
- Vaughan, D. S. 1993. A comparison of event tree risk analysis to Ricker spawner-recruit simulation: An example with Atlantic menhaden. Can. Spec. Publ. Fish. Aquat. Sci. 120:231–241.
- Vaughan, D. S. 1994–1999. Trigger variables for Atlantic menhaden. Annual reports to the Atlantic Menhaden Advisory Committee, Atlantic States Marine Fisheries Commission, NOAA Beaufort Laboratory, Beaufort, North Carolina.
- Vaughan, D. S., and J. V. Merriner. 1991. Assessment and management of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*, stocks. Mar. Fish. Rev. 53(4):49–57.
- Vaughan, D. S., and J. W. Smith. 1988. Stock assessment of the Atlantic menhaden, *Brevoortia tyrannus*, fishery. NOAA Tech. Rep. NMFS 63. Seattle, Washington.
- Vaughan, D. S., and J. W. Smith. 1998. Supplemental analysis of the status of the Atlantic menhaden stock. Report to the Atlantic Menhaden Advisory Committee, Atlantic States Marine Fisheries Commission, NOAA Beaufort Laboratory, Beaufort, North Carolina.
- Vaughan, D. S., and J. W. Smith. 1999. Supplemental analysis of the status of the Atlantic menhaden stock. Report to the Atlantic Menhaden Advisory Committee, Atlantic States Marine Fisheries Commission, NOAA Beaufort Laboratory, Beaufort, North Carolina.