POPULATION AND FISHERY CHARACTERISTICS OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

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ABSTRACT

A stock assessment analysis of the Atlantic menhaden, *Brevoortia tyrannus*, fishery was conducted with purse seine landings data from 1940 to 1981 and port sampling data from 1955 to 1981. Virtual population (cohort) analysis was used to estimate historical stock sizes, rates of fishing, and numbers of recruits. The population exploitation rate (age 1 and older) ranged from 0.29 to 0.51 and averaged about 0.38 for the 1955-79 period. Recruitment at age 0.5 during the 1955-79 period ranged from 1.5 to 18.6 billion fish, with a mean of 5.1 billion. Classical spawner-recruitment relationships describe the data poorly. Growth and mortality data were used to examine yield per recruit for temporal and geographic fishing areas and for the entire fishery. Size at age data, while supporting an earlier hypothesis of density-dependent growth, show a trend toward slower apparent growth in the 1970's than is explained by this hypothesis alone. Yield per recruit of Atlantic menhaden dropped from 107 g for the 1970-72 period to 57 g for the 1976-78 period. A Graham-Schaefer production model estimate of maximum sustainable yield (MSY) for the 1955-79 period was 414,000 metric tons. A modified Pella-Tomlinson production model provided a MSY estimate of 557,000 metric tons. The latter estimate is probably unattainable given current temporal and geographic fishing patterns. Results of these analyses indicate that the Atlantic menhaden fishery suffers from growth overfishing.

Some fishing activity has been conducted on Atlantic menhaden, *Brevoortia tyrannus*, since colonial times, but the purse seine fishery and factory reduction activities began in New England about 1850 (Reintjes 1969). The geographic range of the modern reduction fishery was established by the 1930's (Nicholson 1971a) and the fishery underwent substantial expansion following World War II. Good discussions of the actual fishing operations and types of gear involved are contained in Reintjes (1969) and Nicholson (1971a).

With the exception of the 1950 fishing season, the Atlantic menhaden fishery has dominated total U.S. fishery landings in volume since 1946, when the Pacific sardine, *Sardinops sagax*, fishery was declining. This dominance continued until 1963, when, during its own decline, Atlantic menhaden landings were surpassed by the gulf menhaden, *Brevoortia patronus*, purse seine fishery. Gulf menhaden landings have dominated U.S. fishery landings since, and Atlantic menhaden currently account for about one-third of the total menhaden landings.

The U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries[3] began biological investigations on Atlantic menhaden in 1952. Studies were initiated during what were, in retrospect, peak landing years with the goal to determine the nature of population fluctuations and variability in geographic abundance (June and Reintjes 1959). Following the marked reduction in stock abundance that occurred in the late 1960's, studies were initiated to determine probable causes for the decline and to develop management options to avert a second decline.

The fishery for this migratory clupeid takes place primarily within states' jurisdictional waters (<3 miles from shore), and managerial authority rests with the individual states. Coastwide management plans are cooperatively formulated under the auspices of the Atlantic States Marine Fisheries Commission (ASMFC), but the implementation requires separate legislative or regulatory action by each member state. Individual states are not obligated to act upon cooperatively derived plans or management actions from the ASMFC.

Stock assessment studies provide fundamental scientific information required to formulate coastwide management actions. An early evaluation of the stock status of Atlantic menhaden,

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covering the 1955-68 fishing seasons, was prepared by Henry (1971). Applying virtual population methods (number of fish alive that will be caught in the future (Ricker 1958)) to landings from 1955 to 1969, Schaaf and Huntsman (1972) conducted additional analyses of the population dynamics of this resource. Stock status was again examined with production models using adjusted effort and landings through 1973 (Schaaf 1975a). Population dynamics and potential yield of Atlantic menhaden were further examined by Schaaf (1979), using estimates of numbers landed through the 1976 season; he also employed cohort analysis with Pope's (1972) approximation and the Leslie matrix (after Leslie 1945). In response to a request from the State/Federal Fishery Management Program, Atlantic Menhaden Scientific and Statistical committee, a population dynamics subcommittee was formed (Federal, state, and industry membership). Their report (ASMFC[4]) contained an indepth stock assessment (conducted by the Southeast Fisheries Center (SEFC) Beaufort Laboratory, NMFS) based on landings data through the 1977 season, and was the basis for the Atlantic menhaden management plan adopted by the ASMFC (ASMFC 1981). A computer simulation model of the fishery was developed in an independent analysis and was based on the 1965 through 1978 seasons (Reish et al. 1985; Ruppert et al. 1985). The general concensus of the earlier studies (Henry 1971; Schaaf and Huntsman 1972; Schaaf 1979; ASMFC fn. 4) was that the Atlantic menhaden stock was being overexploited and concern was expressed regarding the reduced spawning stock and/or the high rate of harvest of immature fish.

The primary objective of this report is to evaluate the stock status of Atlantic menhaden through the 1981 season. The more recent 1970-78 fishing seasons are emphasized, notably in presentations of yield per recruit. Effort, landings, and biological sampling data from 1955 through 1981 are used to estimate historic population sizes, age-specific rates of fishing mortality, actual and potential fishery yield, and to examine the spawner-recruitment relationship.

The secondary objective is to determine what historical series of events led to recent conditions in the fishery. This objective can be reasonably met by examining the geographic patterns of harvesting rates and the relative amount of effort expended in each geographic area.

The final objective is to generate some information on the relative abundance and age structure of the menhaden stock during the earlier, presampling period of 1940-54. This is accomplished by comparing, with inferences, the geographic patterns of harvest and effort distribution from the time period with port sampling data (and thus estimates of age-specific exploitation rates) to the patterns of an earlier period when only landings and effort data are available.

OVERVIEW OF LIFE HISTORY AND STOCK STRUCTURE

Hypotheses of the seasonal distribution and migration patterns of adult menhaden were formulated from observations of fish schools (June and Reintjes 1959; Roithmayr 1963) and analysis of age-length distributions (Nicholson 1971b). These hypotheses were later supported by results of tagging studies (Dryfoos et al. 1973; Nicholson 1978). Much of the population is believed to overwinter south of Cape Hatteras to northern Florida, and in late winter begins moving north. By summer, adult menhaden are normally found in dense schools in open coastal waters, bays, and sounds from northern Florida to Maine. These fish schools are stratified by age and size, with the average length and weight increasing with increasing latitude. In September, the most northerly portion of the population begins a southerly movement. During November, most of the adult population that summered in waters north of Chesapeake Bay move south around Cape Hatteras. These larger fish are followed in early December by a southward migration of young of the year that have emigrated from estuarine systems north of Cape Hatteras.

Atlantic menhaden spawning occurs to some degree during virtually the entire year, but not over the entire range at any given time. Evidence for this comes from an ovarian maturation study (Higham and Nicholson 1964) and observed distributions of menhaden eggs and larvae on the continental shelf (Reintjes 1969; Chapoton[5]; Kendall and Reintjes 1975; Judy and Lewis

[4]ASMFC (1980). Report of the Atlantic Menhaden Population Dynamics Subcommittee to the Atlantic Menhaden Scientific and Statistical Committee on the status of the Atlantic menhaden stock and fishery. Unpubl. Rep., 68 p. Atlantic States Marine Fisheries Commission, 1717 Massachusetts Ave., N.W., Washington, D.C. 20036.

[5]Chapoton, R. B. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 76 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

1983). These authors inferred that menhaden spawn in waters north of Long Island from May to September, in the Middle Atlantic Bight south of Long Island from March through May and again in September and October, but primarily spawn in the South Atlantic Bight from October through March.

Menhaden are believed to spawn in neritic waters over most of the continental shelf, as well as in bays and sounds in the Long Island waters and northward (Reintjes and Pacheco 1966; Nelson et al. 1977; Ferraro 1980). Higham and Nicholson (1964) concluded that menhaden do not spawn inside Chesapeake Bay. The buoyant eggs normally hatch in about 2 days, and the larvae have absorbed their yolk sac in about 4 days at a length of about 5 mm (Kuntz and Radcliffe 1917). The larvae subsequently enter estuarine systems when they are 10-34 mm long (June and Chamberlin 1959; Reintjes and Pacheco 1966; Lewis and Mann 1971). The seasonality of larval immigration varies among geographical sites within years and also among years at the same site, owing at least, in part to environmental conditions. Immigration of larvae has been observed from November through April in the South Atlantic Bight, October to June in the Middle Atlantic and Chesapeake Bay areas, and May to October in waters of Long Island and northward (see Reintjes and Pacheco 1966 for literature summary; Lewis and Mann 1971).

Following entry into estuarine waters, larvae progress to lower salinity waters and are frequently found in high abundance in smaller tributary estuaries, where they metamorphose into juveniles at a length of about 34 mm (June and Chamberlin 1959; Wilkens and Lewis 1971; Lewis et al. 1972). Young of the year generally remain in estuaries until the fall when most migrate downstream to larger rivers, bays, sounds, and into the ocean. The range in length of juveniles in the fall has been observed from 40 to 185 mm (Kroger et al. 1974). After their estuarine emigration in the late fall and early winter, juvenile menhaden from New England to the northern portion of the South Atlantic Bight migrate southward in dense schools often very close to shore (surf zone) (Kroger et al. 1971; Kroger and Guthrie 1973).

There are debates whether the Atlantic menhaden population is composed of more than one stock (June 1958, 1965; Sutherland 1963; June and Nicholson 1964; Nicholson 1972, 1978; Epperly 1981). However, the apparently similar movement patterns make what potentially may be genetically different spawning groups inseparable in the fishery. Hence, the menhaden population is currently treated as one exploited and managerial stock.

FISHERY DATA BASE

Records of landings of Atlantic menhaden taken by purse seine and the level of effort expended (vessel weeks) have been collected and maintained back to 1940. Early summaries (through 1971) are available from Nicholson (1971a, 1975) and more recently (through 1984) from Smith et al. (in press) (Fig. 1).

Fishery landings have been sampled and numbers at age landed estimated since 1955. The basic sampling methodology used was described by June and Reintjes (1959), with some recent modifications of sample size (Chester 1984). The efficacy and statistical design of the sampling methods are treated in detail by Chester (1984). The aging technique is described by June and Roithmayr (1960). Estimates of numbers at age landed for the 1955-64 seasons are available by fishing area on an annual basis only and are summarized by Nicholson (1975). Estimates of numbers at age landed used in this report for the 1965-81 seasons were available on a subseasonal basis (weekly) but varied slightly from some published annual summaries (Nicholson 1975 [through 1971]; Schaaf 1979 [through 1976]; and ASMFC 1981 [through 1980]) because of rounding differences, biostatistical error corrections, and use of a different estimation methodology[6]. Smith et al. (in press) gave landings at age values for 1965-84. Values we used were similar except that the 1970-81 values given in Smith et al. (in press) reflect minor corrections to the data file which were made subsequent to these analyses.

Size at age data were available from the port sampling data. Summaries of length and weight by age and geographic area are in Nicholson (1975) and more recently, Smith et al. (in press). Detailed treatment of seasonal length and age distributions by geographic area are contained in Nicholson (1971b, 1972).

[6]Some of the landing estimates (1965-1976) used in the development of ASMFC 1981 were obtained from an estimation procedure which used standardized, noncalendar weeks. While this procedure had some advantages relative to accuracy, it was not fully adaptable to the NMFS port sampling design. It was deemed more desirable to maintain a continuous set relative to estimation procedure. The differences are not large enough to alter analytical conclusions.

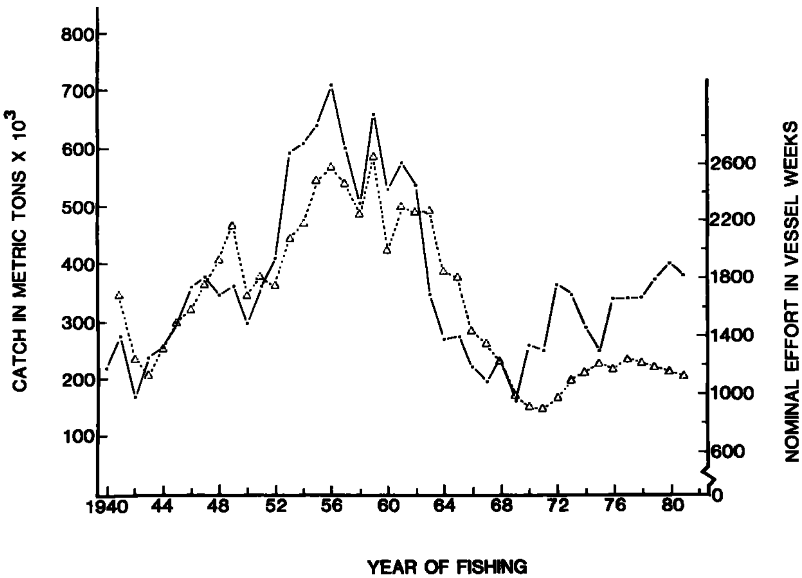

FIGURE 1.—Catch of Atlantic menhaden in thousands of metric tons from 1940 to 1981 (solid line) and fishing effort in vessel weeks from 1941 to 1981 (dashed line). Effort data from 1941 to 1968 are from Nicholson (1971a), catch and effort data from 1968 to 1981 are from Smith et al. (in press).

DESCRIPTION OF THE FISHERY

Geographic Fishing Areas

For purposes of summarization and analysis, June and Reintjes (1959) divided the U.S. Atlantic coast into four geographic fishing areas and one temporal fishing area (Fig. 2). With only a change in the boundary line between the south Atlantic and Chesapeake Bay areas (Nicholson 1975), these divisions have continued to be useful to date.

North Atlantic Area: Waters along the southern coast of Long Island, east of a line due south of Moriches Inlet, and waters northward.

Middle Atlantic Area: Waters west of a line running due south of Moriches Inlet (lat. 40°46′N, long. 72°44′W) on the southern coast of Long Island, southward to Great Machipongo Inlet, VA.

Chesapeake Bay Area: Chesapeake Bay proper and coastal waters south of Great Machipongo Inlet, VA (lat. 37°22′N, long. 75°43′W) to 36°20′N on the North Carolina coast.

South Atlantic Area: Coastal waters of North Carolina south of lat. 36°20′N to Cape Canaveral, FL.

North Carolina Fall Fishery: A temporal fishing area consisting of waters from Cape Hatteras south to the southern border of North Carolina, beginning some time 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 that ends between 8 and 14 November is taken to be the first week of the fall fishery.

Geographic Fishing Seasons

With the exception of state jurisdictional waters in the Chesapeake Bay area, the beginning and ending of seasonal fishing activities were determined by weather and the abundance of fish. Hence, the seasons were somewhat variable. Fishing normally began earlier and ended later in the year in the south Atlantic area, with progressively later beginnings and earlier endings proceeding northward. The south Atlantic (summer) fishery usually began in late March or April and normally ceased in late October or early November. Fishing in waters adjacent to Chesapeake Bay usually began about mid-May and ceased in November, but it occasionally persisted to early December. In the middle Atlantic

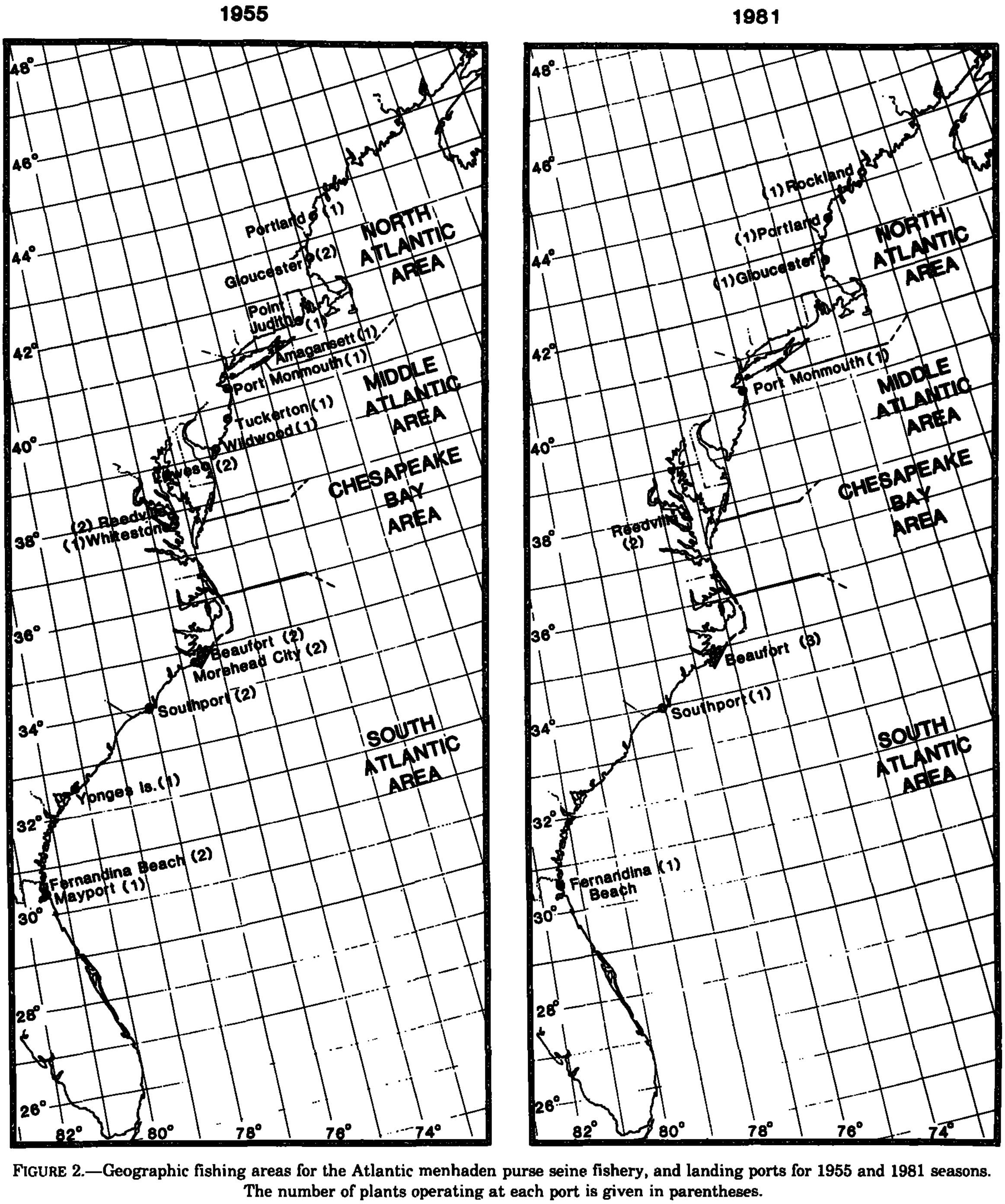

FIGURE 2.—Geographic fishing areas for the Atlantic menhaden purse seine fishery, and landing ports for 1955 and 1981 seasons. The number of plants operating at each port is given in parentheses.

area, fishing usually began about middle to late May and continued into late October. Fishing in the north Atlantic area usually commenced in late May to mid June and continued until mid-September or early October. Current state regulation opens the fishing season in Virginia waters of Chesapeake Bay on the third Monday in May and closes the season on the third Friday in November. All territorial waters of Maryland are closed to purse seine fishing the entire year.

Location and Number of Reduction Plants and Number of Vessels in Purse Seine Fishery

During 1955, 23 plants operated at 16 ports along the U.S. Atlantic coast from Maine to Florida. By 1981 this number had been reduced to 11 plants operating from 8 ports (Fig. 2). The number of vessels landing fish declined from 150 during the 1955 season to 64 by 1967 (Table 1). During 1981, 57 purse seine vessels landed menhaden.

TABLE 1.—Number of purse seine vessels that landed Atlantic menhaden during the fishing year by area, 1955-81 (from ASMFC 1981).

Year	North Atlantic[1]	Middle Atlantic	Chesapeake Bay[2]	South Atlantic[3]	Total[4]	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

[1]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.
[2]Vessels that fished only in regular season. Does not include vessels added in October and November.
[3]Includes only vessels that landed regularly in the summer fishery.
[4]Includes all vessels that landed fish during the year.

Trends in Nominal Effort, Landings, and Age Composition

Since the early 1940's, the Atlantic menhaden fishery has displayed a somewhat classical harvest pattern with an historic increase to a record high, fluctuations, decline, and a secondary slower regrowth (Fig. 1). After an initial slight decline, landings of Atlantic menhaden steadily increased from 167,200 t in 1942 through 1947. Nominal effort generally paralleled landings, but slightly lagged, from a low in 1943 to a minor peak in 1951 and rose to the record high of 712,100 t in 1956. Effort levels increased again in 1953 and reached a secondary peak in 1956 as well. Effort reached its highest level in 1959 with landings at their second highest level of 659,100 t. Landings dropped precipitously from 1962 to a record low 161,600 t in 1969, while effort dropped from 1964 and bottomed in 1971. Although fluctuating, landings showed a net increase from 1970 through 1981. Effort slowly increased up to 1977 and then began a declining trend.

All of the five fishing areas showed a net increase in catches from the 1940's to the peak year in 1956 (Fig. 3). But, the increase was disproportionately distributed between fishing areas. The middle Atlantic area showed the greatest relative increase, followed by the north Atlantic and Chesapeake Bay areas, with the south Atlantic and North Carolina fall fishery only showing slight increases (Fig. 4). While 1956 represented the year of peak landings for the fishery, only the middle Atlantic catches peaked during this year.

The increase in fishing effort expended during the 1940's to the mid-1950's was also disproportionately distributed between fishing areas, with the middle Atlantic showing the greatest increase, followed by the north Atlantic (Fig. 5). The Chesapeake Bay area showed a slight increase, while the south Atlantic and North Carolina fall fishery areas showed little, if any, actual increase in nominal effort.

Following 1956, the proportion of the catch taken in the middle Atlantic area decreased relative to the proportion of effort expended in that area. After 1962, effort (and catches) rapidly decreased in the middle Atlantic area, with both the effort and catches seemingly shifted to the Chesapeake Bay area (Figs. 4, 5). This was a relatively dramatic shift, considering that the middle Atlantic catch was generally dominated by age-2 and -3 fish while Chesapeake Bay catches were dominated by ages 1 and 2. Additionally, middle Atlantic fish were generally larger for any given age than those from Chesapeake Bay. Catches and effort also decreased in the north Atlantic area during the same time frame.

The Atlantic menhaden stock probably had its strongest and broadest age structure in 1955 and 1956, which also represent the first years when port sampling covered the full geographic range

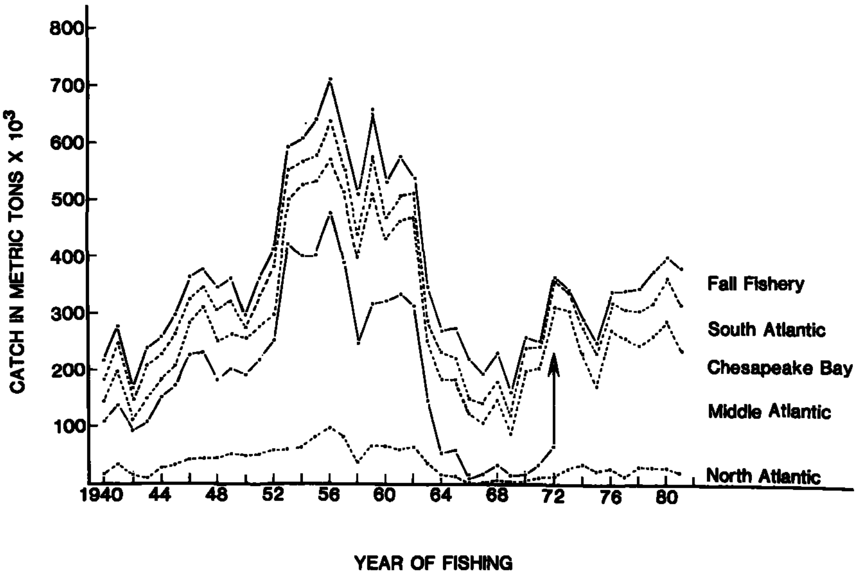

FIGURE 3.—Contribution to landings of Atlantic menhaden by fishing area and season in thousands of metric tons for years 1940-81. The middle Atlantic and Chesapeake Bay area landings are combined after 1972 due to confidentiality restrictions.

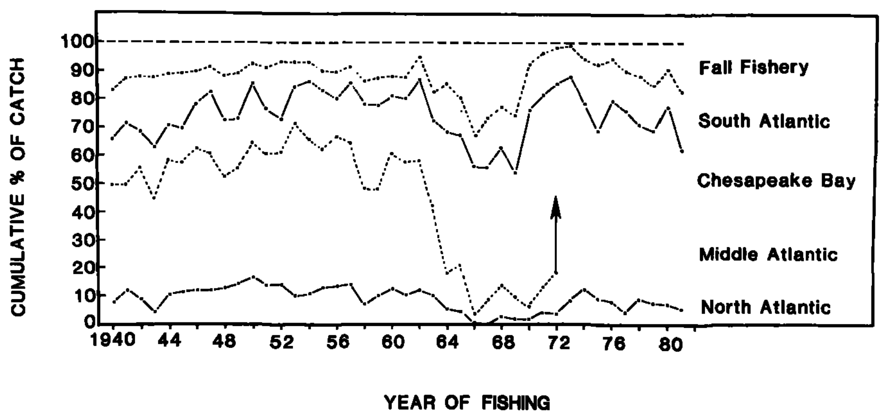

FIGURE 4.—Cumulative contribution by percent total landings of Atlantic menhaden by fishing area for years 1940-81. The middle Atlantic and Chesapeake Bay area values are combined after 1972 due to confidentiality restrictions.

of the fishery (Fig. 6). The number of older fish in the population was somewhat reduced by 1959, but showed a slight recovery in 1960. The age structure became markedly constricted by 1965, and drastically truncated by 1967. The age structure appeared to begin broadening slowly about 1972, and appears to be continuing this trend through 1981.

Although a few individuals aged 9 and 10 years were taken by the fishery during the late 1950's, the maximum age class with adequate representation for computational purposes is age 8. (Hence, the age category of 8+ is taken in this report to be age 8, which for most years contained only age-8 fish.) Individuals age 8+ were represented in landings from 1955 through 1966 fishing seasons. From 1967 through 1969 the oldest fish were age 6, and likewise; 1970 through 1974, 1976, and 1978, age 5; and again, 1975 and 1977, and 1978 through 1981, age 6.

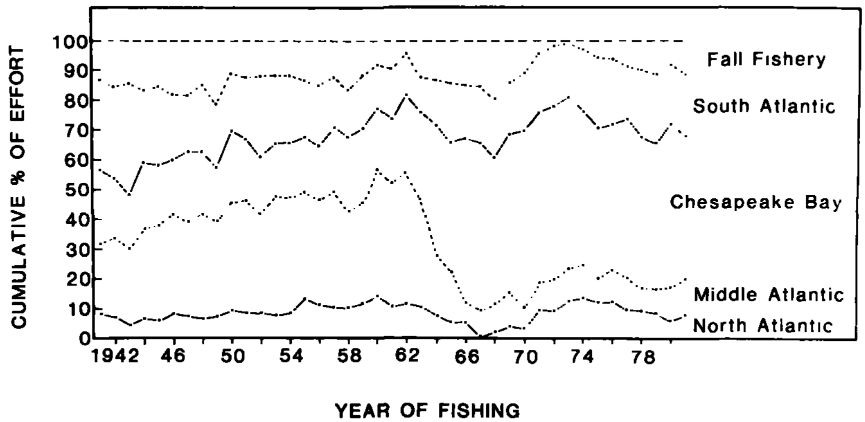

FIGURE 5.—Cumulative fishing effort on Atlantic menhaden as a percent of total, by fishing area for years 1941-81. (Data for 1941 through 1968 were adjusted (reduced) by Nicholson (1971a) to compensate for the small size of vessels that frequently fished in that area. The data for the middle Atlantic area were also adjusted, but to a lesser degree. Data from 1969 to 1981 are unadjusted. North Atlantic area data, adjusted by the Nicholson (1971a) criteria, would probably be less than half the amount shown, while the middle Atlantic area values may only be slightly reduced.)

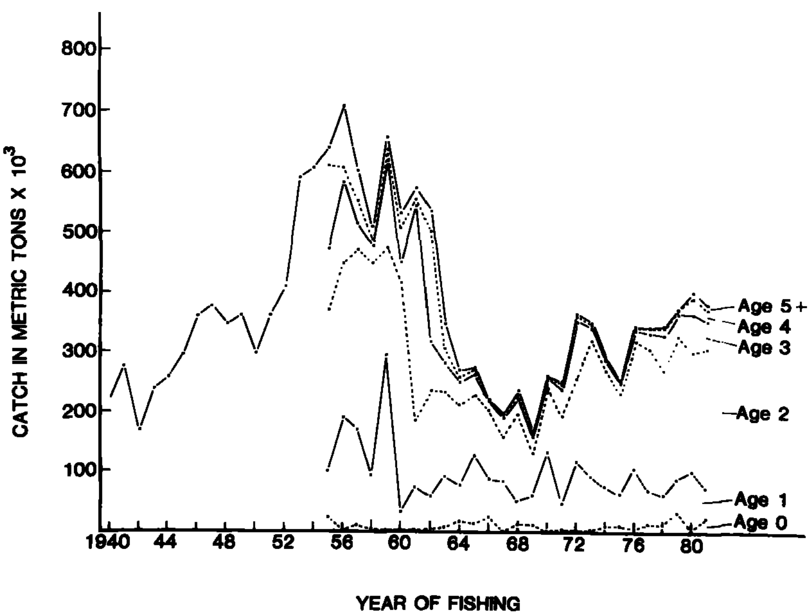

FIGURE 6.—Catch of Atlantic menhaden in thousands of metric tons by age group for 1955 to 1981.

SIZE AT AGE AND GROWTH ANALYSIS

It is necessary to derive two types of size at age and growth estimates because of the seasonal differential distribution of Atlantic menhaden by age and size (Nicholson 1972, 1978). Parameters are estimated by area to characterize the segments of the population normally harvested within that area and are estimated for the entire fishery to characterize the harvested population. Because relative harvest rates may vary among areas between seasons, apparent area-specific growth parameters are estimated for yield-per-recruit analyses. On the other hand, parameters generated in each area are inappropriate (biased) for describing the entire population (or fishery). For example, growth rates and average size at age values for the north Atlantic area will be greater than those for the population, and similarly values estimated for the south Atlantic will be less than true population values. (The only exception is the North Carolina fall fishery, which apparently harvests a reasonably well-mixed migratory population.)

Size at age and growth estimates for the entire stock are needed for yield-per-recruit analysis for the entire fishery and to ascribe an average size at age for the spawning stock for each year. These estimates are obtained by appropriately weighting the sampling results from each fishing area, as will be shown.

Additionally, since growth of Atlantic menhaden has been shown to be inversely related to year class size (density-dependent) (ASMFC fn. 4), a condition predicated during the estuarine portion of the life cycle (Reish et al. 1985), growth equations must be computed for each year class. The fishing season is divided into quarterly increments for these analyses (Table 2). The analytical steps taken to obtain these size estimates and how they are used follows.

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

Quarter	Beginning week ending date	Ending week ending date
1	≥ 3/01	≤ 5/30
2	≥ 5/31	≤ 8/29
3	≥ 8/30	≤ 11/28
4	≥11/29	≤[1]4/29

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

Area-Specific Mean Size at Age and Growth Rates

Mean lengths at age by area by quarter for each of the 1965-81 seasons were estimated directly from the port sampling data as unweighted arithmetic means. These results were in turn arranged by specific year class and fitted to the von Bertalanffy growth equation using the computer package BGC3 (Abramson 1971). It was assumed that each mean length estimate was representative of the middle of the quarterly interval, i.e., for the first quarter (age X.0-X.25) the mean value is assigned to age X.125, etc. These fitted area-specific von Bertalanffy parameters were used to derive estimates of length at age for the beginning of each time interval. These estimates were in turn converted to estimates of weight at age for the area-specific yield-per-recruit analysis.

Mean Size at Age and Growth for the Entire Fishery

Predictive equations for growth which are representative of the population as a whole (entire fishery) are needed to estimate size at age for the spawning stock and for yield-per-recruit analysis of the entire fishery. For years 1965 to 1981, mean lengths at age by quarter for the entire fishery were obtained by weighting each area's estimate of mean length by its corresponding catch in numbers at age by quarter. Age 0.875 (fourth quarter age 0) was the youngest age for which mean length was calculated. These values were arranged by year class and were fitted to the von Bertalanffy growth equation.

Estimates of weighted mean length by quarter could not be calculated for the fish caught before 1965 because estimates of numbers at age landed by quarter by area were not available even though size at age is available weekly. Since much of the fourth quarter catch of the North Carolina fall fishery is composed of migratory stocks, it was presumed that a representative estimate of length at age for the entire population might be obtained from the fourth quarter values from this area alone. To test this hypothesis, mean lengths for the 1965 to 1978 year classes from the fourth quarter in the North Carolina fall fishery were fitted to the von Bertalanffy growth equation. The resultant curves were compared visually with results when all weighted mean length values were used. The results were quite similar when five or more data points were available and dissimilar to relative degrees when <5 data points were available. Because all year classes from 1955 to 1964 had at least 5 data points which met the above criteria, von Bertalanffy curves were fitted to these values (Table 3).

Weight-Length Relationship

The predictive growth equation used in this report uses length at age. Weight-length relationships were derived to estimate weight at age values. The greatest potential within year variation in weight-length parameters is expected among

TABLE 3.—Estimated von Bertalanffy growth parameters for Atlantic menhaden, year classes 1955-78.

Year class	L_∞	K	t_0	n (means)	Age range (years)
1955[1]	339.49	0.5401	0.1234	7	0-7
1956	343.67	0.4598	0.0245	7	0-8
1957	324.49	0.6260	0.0707	7	0-7
1958	363.73	0.3637	−0.1163	7	0-7
1959	355.64	0.3631	−0.4709	6	0-6
1960	354.69	0.4009	−0.1481	5	0-5
1961	340.52	0.4514	−0.3506	5	0-5
1962	376.35	0.4012	−0.1122	5	0-5
1963	370.04	0.3494	−0.4652	6	0-6
1964	331.17	0.6138	0.0606	5	0-5
1965[2]	404.13	0.3187	−0.3529	17	0-6
1966	367.15	0.4575	−0.0645	18	0-6
1967	375.81	0.4539	0.1815	16	0-5
1968	415.22	0.2813	−0.7318	16	0-5
1969	356.19	0.5868	0.0530	18	0-6
1970	348.00	0.5351	0.0034	16	0-5
1971	356.82	0.4103	−0.2772	18	0-6
1972	316.74	0.6058	0.0767	17	0-5
1973	341.53	0.3884	−0.2947	20	0-5
1974	325.60	0.4329	−0.1280	22	0-6
1975	420.86	0.1779	−1.1445	21	0-6
1976	393.73	0.2410	−0.4372	20	0-5
1977	528.99	0.1455	−0.8354	16	0-4
1978	246.54	0.5807	−0.3399	12	0-3

[1]Year classes 1955-64 represented by fitted values for 4th quarter, area 5 (see text).
[2]Year classes 1965-78 represented by fitted values for weighted quarterly mean lengths.

quarters. Because each area (except perhaps area 5) contains a limited portion of the range of sizes extant in the menhaden population, the weight-length relationship is estimated across areas, but within quarters. Annual variation was also assumed to exist, thus parameter estimates were calculated for each fishing season where subsequent yield-per-recruit analysis was intended (1970-78) using $\log_e$ transformed data and least squares regression (Table 4).

Annual Mean Weights Weighted by Catch

Estimates of annual weighted mean weight by age of Atlantic menhaden in purse seine catches were calculated to permit computations of age-specific and year class-specific biomass contributions to landings. Weighted mean weight for the entire fishery was calculated from the average weight by age by season for each of the five recognized areas of the fishery and then weighted by the estimated numbers caught by age in each respective area. These data were derived directly from the port sampling data and are not from von Bertalanffy derived lengths converted to weights.

VIRTUAL POPULATION ANALYSIS

Virtual population analyses (VPA's) were conducted to reconstruct population sizes and estimate rates of fishing mortality. Analyses were conducted on all age groups of the 1947-78 year classes which were represented in the 1955-81 landings. The backward sequential computations were performed using the computer program MURPHY written by Tomlinson (1970).

Instantaneous Rate of Natural Mortality

The estimate of the annual instantaneous rate of natural mortality (M) used in this report was 0.45. Early estimates were from catch statistics, 0.37 (Schaaf and Huntsman 1972); from preliminary tag-recovery analysis, 0.52 (Dryfoos et al. 1973); and from a more extensive tag-recovery analysis, 0.50 (mean of age-specific rates for ages 2 and 3) (Reish et al. 1985). The 0.45 value represents a mean of the range of available estimates. The implications of the selection of 0.45 for M are addressed.

Temporal Organization of Analyses

The time periods used in these analyses (Table 2) closely correspond to critical life history and fishery events. The birth date for a year class, and the beginning of a new fishing season for Atlantic menhaden, is 1 March. Because of the protracted spawning season of menhaden, young of the year may have been spawned as early as the previous August and as late as the following May or June, but most of the spawning takes place in the fall and winter (Nelson et al. 1977). The beginning of the fourth quarter (week beginning ≥ Nov. 29) is used as a finite date to estimate spawning stock size. Thus, the spawning stock in the fall (beginning of the fourth quarter) of the previous calendar year (age X.75) is defined to be the parental stock for a subsequent (1 March) year class. Recruitment is examined at age 0.5 (beginning of third quarter, age 0) and at age 1.0 (beginning of first quarter, age 1).

Three sets of VPA's were conducted with the length of the time intervals varied between sets. The first set provided the basic estimates for reconstruction of the historical population and the estimates of rates of fishing mortality. This series was done on an annual basis and involved all subject year classes. These estimates are used pri-

TABLE 4.—Weight-length regression parameters for Atlantic menhaden, by quarter and year, 1970-81 seasons ($\ln W = a + b \ln L$).

Fishing	Quarter 1		Quarter 2		Quarter 3		Quarter 4		Annual	
years	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
1970	−11.9324	3.1924	−11.5760	3.1224	−11.3909	3.0971	−11.5124	3.1087	−11.6666	3.1421
1971	−10.8692	2.9838	−11.0121	3.0135	−11.4336	3.0941	−12.0821	3.2044	−11.3620	3.0786
1972	−13.0384	3.3809	−11.5388	3.1072	−11.5989	3.1131	−11.5413	3.1028	−11.6553	3.1264
1973	—	—	−10.6360	2.9401	−10.7756	2.9741	−11.4291	3.0889	−10.9727	3.0060
1974	−12.8892	3.3503	−11.3321	3.0695	−11.2386	3.0552	−12.1803	3.2310	−11.4423	3.0896
1975	−10.3727	2.9027	−11.9798	3.1950	−11.7856	3.1555	−11.6995	3.1388	−11.8524	3.1703
1976	−10.9908	2.9972	−12.5123	3.2945	−12.4698	3.2933	−11.9663	3.1873	−12.3503	3.2642
1977	−12.6133	3.3110	−12.9689	3.3856	−11.9884	3.2043	−12.0643	3.2109	−12.5865	3.3137
1978	−12.3304	3.2666	−12.5737	3.3096	−12.0319	3.2124	−11.8477	3.1642	−12.3324	3.2653
1979	−11.9230	3.1950	−11.8170	3.1701	−12.0982	3.2243	−12.5516	3.2900	−12.4043	3.2793
1980	−12.2804	3.2580	−12.8763	3.3696	−11.9109	3.1884	−11.7750	3.1547	−12.3969	3.2792
1981	−12.2049	3.2386	−12.4031	3.2765	−12.6597	3.3215	−11.9663	3.1747	−12.5365	3.3004

marily in discussions of the impact of nominal effort and for modification of input variables for surplus production analysis.

The second series, with shorter time intervals, permitted a more precise apportioning of fishing mortality between fishing areas within a fishing season and provided within season estimates of numbers at age present in the population. This series was conducted on a quarterly basis and included the 1965-78 year classes. These estimates permitted a reconstruction of the fishery for the 1970-78 seasons which forms the basis of the subsequent yield-per-recruit analyses. The quarterly estimates of numbers at age are also used to estimate numbers of recruits for the 1965-78 year classes and the numbers of spawners that were ultimately derived from these year classes.

The third series was conducted to estimate numbers of recruits and their parental spawning stock for the 1955-64 fishing seasons. This series included the 1947-64 year classes and used mixed length time intervals. A 1/2-yr interval, which included ages 0.50 and 0.75 (quarters 3 and 4), was used to provide estimates of numbers of age-0.5 individuals present in the population. The time interval for age-1 fish was annual. Intervals for age-2 and older individuals were alternately three quarters of a year (quarters 1-3), corresponding to ages X.0-X.50, and one quarter of a year (quarter 4), corresponding to age X.75. This temporal construction of the numbers at age data required several adjustments which are discussed.

Additional VPA's were conducted to examine the sensitivity of results to the value of natural mortality used (0.45) and to the initial estimates of fishing mortality rates. A series of annual VPA's were conducted for the 1955-78 year classes with $M = 0.35$ and $M = 0.55$, which encompass the range of available estimates discussed earlier. Additional annual runs were conducted with varied starting F's for the 1955 year class, which for reasons discussed later, potentially represents a worst case situation relative to rates of convergence of estimates.

VPA Numbers at Age Landed Data Sets

The annual estimates of numbers at age caught were rearranged from a seasonal format to a year-class format. For the quarterly runs, the weekly catch at age estimates were summed to quarters and rearranged by year class. The mixed time interval VPA data sets were derived from the annual set, and thus required some approximations and adjustments to obtain a subyear format. Annual catches of age 0 (1955-64 seasons) were assumed to be in quarters 3 and 4 since the bulk of the age-0 catches occurred after 30 August (beginning of the third quarter). The major portion, if not all, of the catches of age-2+ fish (spawning ages) that were made during the fourth quarter time interval, was in the North Carolina fall fishery. During the 1965-69 fishing seasons, an average of 58% of the age-2+ fish that were landed in the fall fishery were landed during the fourth quarter. Hence, 58% of the fall fishery landings of age-2+ fish of the 1947-64 year classes were assumed to have been taken during the fourth quarter. The remainder of the total annual catch was assigned to the single three-quarter time interval (quarters 1-3). The time period used for the age-1 fish remained annual, so no adjustments were required.

Estimates of Initial Annual Rate of Instantaneous Fishing Mortality

Although a single method of estimation for the starting instantaneous annual fishing mortality rate (F) for backward calculations in VPA is desirable, a few year classes required alternate approaches. Year class-specific catch curves were examined visually. All years of age from the oldest to youngest that lie within a reasonably straight portion of a semilogarithmic catch plot were $\log_e$ transformed and regressed against age. The slope was taken as an estimate of $-Z$ (total instantaneous mortality) and by subtracting M a "general trend" F was obtained. Starting F's were obtained by this method for all year classes except 1947, 1948, 1949, 1954, 1966, 1971, 1974, and 1978. Since only 2 years of landings after full recruitment were available for the 1978 year class, an estimate of Z was made: $-\log_e$ (catch in numbers of age 3/catch in numbers of age 2). The estimate for 1949 was obtained similarly using ages 7 and 8. The 1954, 1966, 1971, and 1974 year classes experienced an apparently higher fishing rate during their last year in the fishery compared with that experienced 1 year earlier. Thus, starting F's were obtained from average VPA results from several other age classes caught in the same year. Starting F for age 8 of the 1954 year class was estimated as the mean F for ages 5-7 (year classes 1955-57) caught in the same 1962 season. Initial F for age 5 of the 1966 year class was the annual VPA estimate of age 4 from the 1967 year class. Similarly, starting values of F for the 1971 and 1974 year classes were the means of the same fishing season age-4 and age-5 values for the 1972 and 1973, and 1975 and 1976 year classes. Starting F's on age 8 for the 1947 (one age class represented) and 1948 (two age classes represented) year classes were means of similar fishing season VPA F's for ages 5-7. The initial annual F values and their sources for VPA are summarized in Table 5.

Conducting the VPA computations for the annual series was straight forward, as the trial F's were annual. The quarterly series and mixed time interval series required trial and error runs. Trial starting F's for these VPA's were adjusted downward until the sum of the F's within the last year (oldest fish of the year classes) were ±0.5% of the initial annual F estimate for each year class (Table 5).

Except for the sensitivity computations, the general results of the VPA's are presented and discussed where they are subsequently used. Using a relatively wide range of starting values for the 1955 year class, estimates of age-specific F and numbers at age present at the beginning of a season (Fig. 7) converged quite rapidly to similar values for the (younger) ages which dominate the fishery in both numbers and biomass (Figs. 8, 9). This is expected because of the relatively high rates of fishing mortality exerted on the stock (Ulltang 1977). The lower the exploitation rate, the slower the values will converge. The 1955 year class had the lowest starting F of any year class (Table 5) (other than 1947 which had only one age class represented) and relatively low to moderate rates of exploitation on all age classes. Thus the estimates for the other year classes should converge more rapidly than the one shown. Since it is highly unlikely that the initial estimates of F differ from true values to the extreme degrees tested, the VPA estimates used

TABLE 5.—Estimates of initial F for annual virtual population analyses (VPA's) of Atlantic menhaden, source of estimate, and ages involved, by year class.

Year class	Initial F	VPA's ages	Regression ages	Mean from VPA results[1]
1947	0.4862	8	—	yes
1948	1.3134	7-8	—	yes
1949	1.3498[1]	6-8	—	—
1950	1.6504	5-8	6-8	—
1951	0.9243	4-8	4-8	—
1952	0.8590	3-8	5-8	—
1953	0.8620	2-8	2-8	—
1954	1.1645	1-8	—	yes
1955	0.7006	0-8	2-8	—
1956	0.8557	0-8	2-8	—
1957	1.0651	0-8	5-8	—
1958	1.8497	0-8	4-8	—
1959	1.4325	0-7	3-7	—
1960	1.7620	0-6	2-6	—
1961	3.0108	0-6	4-6	—
1962	1.9074	0-6	2-6	—
1963	2.0482	0-6	2-6	—
1964	2.1116	0-5	2-5	—
1965	2.7386	0-5	3-5	—
1966	1.6194	0-5	—	yes
1967	1.1191	0-5	2-5	—
1968	1.6677	0-5	2-5	—
1969	1.9585	0-6	3-6	—
1970	2.2554	0-5	2-5	—
1971	1.5437	0-6	—	yes
1972	1.7143	0-5	2-5	—
1973	1.5403	0-5	2-5	—
1974	1.4321	0-6	—	yes
1975	1.3185	0-6	2-6	—
1976	1.0167	0-5	2-5	—
1977	1.3079	0-4	2-4	—
1978	1.4391	0-3	—	—

[1]See text.

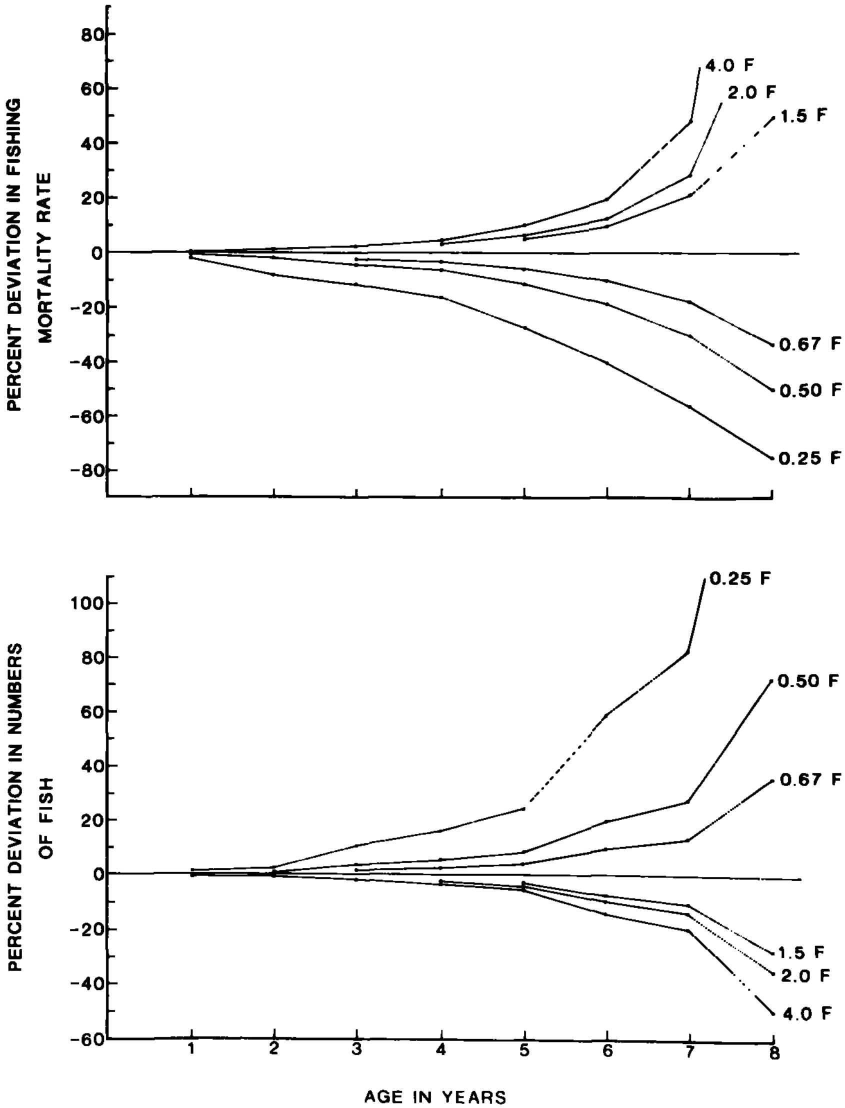

FIGURE 7.—Deviations in annual VPA (virtual population analysis) estimates of numbers at age present in the population and age specific fishing mortality rates for Atlantic menhaden resulting by varying the initial rate of annual F by the multiples shown. The estimates are for the 1955 year class (initial F = 0.7006).

here should be considered reasonably precise (and stable) relative to the initial F values.

Since F and M are additive with respect to Z, errors in these computations resulting from an incorrect selection of the rate of M are additive with respect to subsequent estimates of F, and estimates of numbers at age present in the population will differ in a proportional fashion. In other words, if our selection of the estimate of M is too great, numbers at age are overestimated, and if M is too low, the reverse is true (Fig. 10). Similarly, estimates of year class size vary by a nearly constant proportion (Fig. 11). The range of available estimates of M is relatively narrow, hence it is unlikely that conclusions reached in this report would be altered even if the estimate of M for these analyses were allowed to vary randomly within these bounds between years.

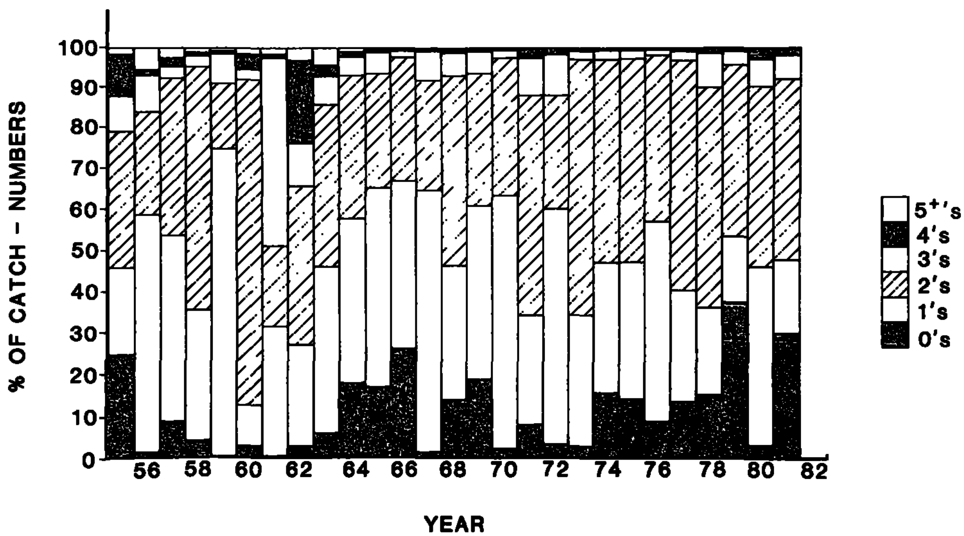

FIGURE 8.—Contribution in percent of total numbers of Atlantic menhaden landed by age group, from 1955 to 1981.

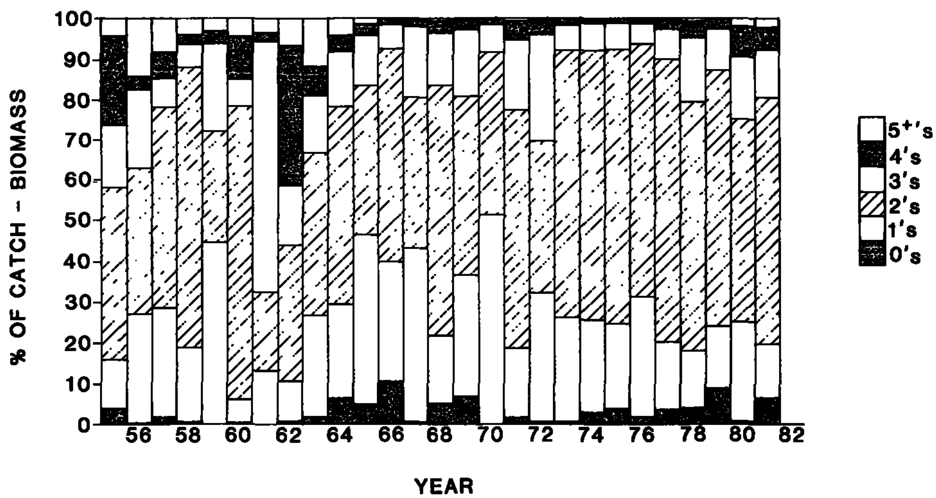

FIGURE 9.—Contribution in percent of total biomass of Atlantic menhaden landed by age group, from 1955 to 1981.

SPAWNER-RECRUITMENT RELATIONSHIP

Estimates of Numbers of Spawners

Higham and Nicholson (1964) concluded that a few age-1 Atlantic menhaden and most age-2 fish are sexually mature by the end of the season. The simplifying assumption for purposes of estimating spawning stock in these analyses is that no age-1 fish and all age-2 fish are mature by the beginning of the fourth quarter. This assumption was also used in other studies (Nelson et al. 1977; ASMFC fn. 4; Schaaf and Huntsman 1972).

Estimates of the number of fish age 2.75 and greater alive at the beginning of the fourth quarter of any given year n comprised the parental spawning stock for year class $n + 1$. The estimates of number of spawners resulting from the 1947-64 year classes were obtained from the mixed time-interval VPA series. The number of spawners from the 1965-78 year classes were ob-

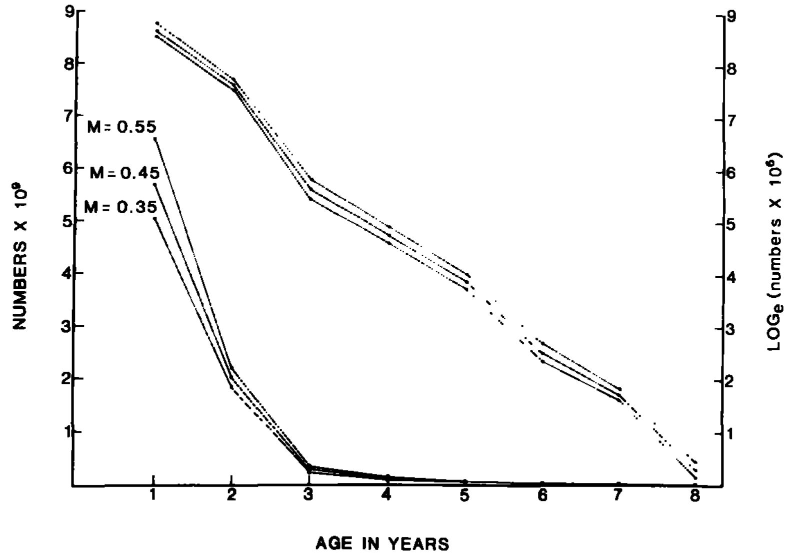

FIGURE 10.—VPA (virtual population analysis) estimates of numbers at age present in the Atlantic menhaden population for the 1955 year class for three levels of natural mortality (lower left), and natural logarithms of these same numbers at age (upper right).

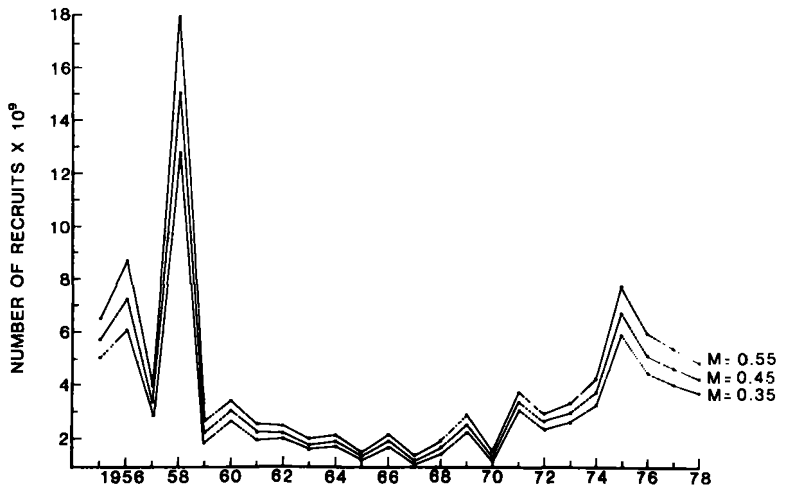

FIGURE 11.—Annual VPA (virtual population analysis) estimates of numbers of Atlantic menhaden recruits at age 1 for three levels of natural mortality.

tained from the quarterly VPA series. These estimates were rearranged to correspond to fishing seasons (Table 6). There were no estimates for numbers at age landed in the 1954 North Carolina fall fishery. Hence, the parental spawning stock for the 1955 year class was obtained by using 1955 estimates for age X.0 and back-calculating numbers at age to the beginning of the 1954 fourth quarter (age (X − 1).75) with mean fourth quarter survival rates at age for fishing years 1955-57. An additional adjustment was made to complete the estimates of spawning stock size. If an age group was represented during quarters 1-3 but not in quarter 4 of the last year it

TABLE 6.—Estimates of spawning stock size in thousands by age for Atlantic menhaden, 1954-81 seasons, at start of the fourth quarter of each fishing season.

	Age						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75+
1954[1]	720,068.8	966,532.5	158,421.1	44,416.7	10,592.6	2,383.0	NE
1955	750,253.7	216,441.3	325,276.2	50,554.4	12,061.1	3,463.6	932.1
1956	285,976.8	213,151.0	102,272.1	98,950.9	11,254.9	2,541.6	593.9
1957	321,399.1	99,134.2	72,526.3	35,097.5	19,882.5	1,250.7	362.0
1958	1,060,499.7	145,248.4	46,161.4	29,036.6	11,021.2	5,504.1	82.2
1959	330,845.0	366,056.3	65,942.6	19,506.9	7,873.1	2,094.9	1,339.2
1960	2,662,230.0	144,140.8	125,048.6	20,387.2	5,552.2	1,337.9	693.7
1961	432,466.5	736,311.5	69,834.8	46,372.7	6,667.1	1,300.3	144.1
1962	215,894.3	84,439.3	97,991.5	18,987.4	6,579.9	1,795.1	258.7
1963	173,757.5	43,433.2	17,968.5	15,709.5	2,756.5	991.8	539.0
1964	151,149.8	26,764.3	4,358.7	2,199.5	1,112.9	157.6	194.2
1965	101,340.2	12,848.1	1,419.3	164.1	180.0	53.7	13.2
1966	194,222.2	18,780.6	1,401.8	15.5	18.0	27.4	5.4
1967	133,362.5	36,015.8	2,858.6	207.1	0.5	0	0
1968	122,033.7	16,235.3	1,227.0	199.0	8.1	0	0
1969	125,131.1	26,492.8	761.0	16.4	1.1	0	0
1970	175,837.2	34,303.4	6,017.2	48.1	0	0	0
1971	265,058.8	29,169.5	4,107.8	619.4	0	0	0
1972	64,386.9	14,863.7	1,187.3	766.8	0	0	0
1973	80,116.3	5,210.6	2,021.8	142.9	0	0	0
1974	94,348.3	7,760.3	241.5	153.0	0	0	0
1975	140,817.4	12,947.3	356.3	12.9	13.8	0	0
1976	212,735.5	37,466.2	2,306.5	164.1	0	0	0
1977	498,135.8	59,415.2	5,630.1	245.6	22.3	0	0
1978	451,889.2	80,962.9	13,390.0	927.6	0	0	0
1979	486,903.4	155,932.5	26,789.6	2,772.6	47.3	0	0
1980	424,606.5	103,707.0	42,254.5	4,995.9	909.8	0	0
1981	-No. est.-	57,691.0	14,868.6	7,335.7	397.5	0	0

[1]Derived from 1 March 1955 estimates (see text).

appeared in the fishery, it was assumed that some representatives were still present in the population at the beginning of quarter 4 (age X.75). Estimates of numbers present were obtained by a forward calculation using the mortality estimates of the previous interval obtained from the VPA's.

Estimates of Potential Egg Production

The age structure of the Atlantic menhaden population varied substantially during the time period under study. Therefore, an alternate method of examining spawning stock (i.e., potential egg production) as used by Nelson et al. (1977) was employed.

Sizes at age X.75 for spawners derived from the 1955-78 year classes were calculated from the von Bertalanffy growth parameters derived earlier for the entire fishery (Table 3). However, because of insufficient data, growth curves were not fitted to the 1947-54 year classes, so observed mean lengths at age during the fourth quarter were used for the spawners derived from these year classes. If the fourth quarter length at age was not available, means from the nearest three year classes were used.

Estimates of egg production were obtained from the expression used by Nelson et al. (1977), which was derived from data of Higham and Nicholson (1964):

$$\ln(E) = 0.3149 + 0.0176L$$

where, E = thousands of eggs produced per female, and
L = estimated fork length.

This equation was used with estimated mean length at age X.75 for fish 2 years and older. Assuming a 50/50 sex ratio, potential egg production by age by season was obtained by multiplying the values per female by number of females at age (Table 7).

Estimates of Numbers of Recruits

Estimates of the number of recruits for each year class were obtained from the results of the VPA's. The year class-size estimates for 1955-64 are from the mixed time-interval analyses and

TABLE 7.—Estimated number of recruits by year class at age 0.5 and 1.0, estimated number of spawners that produced the year class, and estimated egg production from the spawning stock, for Atlantic menhaden.

Year class	Number of recruits × 10³ Age 0.5	Age 1.0	No. of spawners × 10³	No. of eggs × 10¹²
1955	7,888,342	5,621,258	1,902,414.7	219.659
1956	8,999,656	7,153,549	1,358,982.4	147.047
1957	4,419,989	3,263,196	714,741.2	83.977
1958	18,612,316	14,767,294	549,652.3	57.768
1959	2,722,999	2,164,428	1,297,553.6	143.822
1960	3,786,692	2,958,923	793,658.0	76.642
1961	2,769,147	2,210,534	2,959,390.4	156.058
1962	2,841,268	2,222,880	1,293,097.0	106.781
1963	2,304,564	1,754,140	425,946.2	37.508
1964	2,764,796	1,938,001	255,156.0	21.466
1965	2,072,852	1,430,539	185,937.0	13.806
1966	2,879,544	2,001,871	116,018.6	7.552
1967	1,522,438	1,209,954	214,470.9	17.017
1968	2,319,215	1,710,666	172,444.5	13.053
1969	3,448,326	2,611,940	139,703.1	11.240
1970	1,755,217	1,382,032	152,402.4	12.056
1971	4,513,962	3,539,073	216,205.9	17.594
1972	3,516,016	2,760,443	298,955.5	31.279
1973	3,908,494	3,085,954	81,204.7	8.044
1974	5,197,484	3,866,593	87,491.6	6.076
1975	9,024,340	6,932,136	102,503.1	6.591
1976	6,953,329	5,297,439	156,147.7	7.575
1977	6,619,024	4,827,413	252,672.3	11.966
1978	6,040,678	4,404,267	563,449.0	18.864
1979[1]	10,322,177	6,890,589	547,169.7	18.389
1980	NE	NE	672,445.4	26.045
1981	NE	NE	576,473.7	22.294

[1]Preliminary estimates.

those for 1965-78 are from the quarterly analyses. Estimates of recruitment were computed for both age 1.0 and age 0.5 (Table 7). Estimates at age 1.0 are provided for comparative purposes, as this age has been frequently used for studies on Atlantic menhaden (ASMFC fn. 4). Age 0.5 is used here to appropriately credit a year class with the numbers of juvenile fish removed from the population by the fishery during the fall and early winter. Although perhaps underestimates because the value of M (0.45) may be too low for fish younger than 1-yr old, these estimates are relatively consistent.

The degree of dependency of the number of recruits on the size of the parental stock has been examined by Schaaf and Huntsman (1972), Nelson et al. (1977), Schaaf (1979), and Reish et al. (1985). All earlier workers employed the Ricker (1954) model, but Reish et al. (1985) also used the Beverton and Holt model as well as the unnormalized gamma function. The published results indicate weak relationships, with substantial variability about both fitted models. Nelson et al. (1977) developed a multiple regression model to explain observed deviations from the Ricker model attributable to several annually varying environmental parameters, primarily Ekman transport, which would affect the oceanic larval stage.

The spawner-recruitment data (Table 7) were fitted with both the Ricker and Beverton-Holt models using a nonlinear least squares method (Marquardt's (1963) algorithm). Both models fit the data poorly (Fig. 12). The Beverton-Holt model is slightly better than the Ricker model if residual sum of squares is used as a goodness of fit criterion. The Beverton-Holt residual is only slightly less than that about a mean value, which assumes no relationship between numbers of spawners and numbers of recruits. Residual sum of squares in the Ricker model was slightly greater than results for the mean.

POTENTIAL AND ACTUAL YIELD

Production Models

The application of production models to the Atlantic menhaden purse seine fishery is hampered on theoretical grounds by two major conditions: 1) the fishery has not been operating under equilibrium conditions, and 2) fishing effort is not proportional to fishing mortality (F). The catchability coefficient (q) is inversely related to population size (Schaaf 1975b). Schaaf and Huntsman (1972) and Schaaf (1979) circumvented this latter problem by adjusting effort to a base year.

The effects of this problem were reduced in this analysis by using an estimate of population F for the independent variable instead of adjusting effort (Nelson and Ahrenholz 1986). To estimate a population rate of fishing mortality (F_{pop}), estimates of the population sizes (excluding 0-age fish) at the beginning of each fishing season from 1955 to 1979 were reconstructed from annual VPA estimates. These were in turn divided into the estimated catch in numbers (excluding age 0), to obtain an estimate of population rate of exploitation (U_{pop}). By trial and error, estimates of F_{pop} were obtained for each fishing season from $F_{pop} = U_{pop} Z/(1 - e^{-Z})$, assuming $M = 0.45$ (Table 8).

A Graham-Schaefer curve was fitted to the catch and population fishing mortality data by Marquardt's (1963) algorithm. This procedure produced an MSY (maximum sustainable yield) estimate of 414,000 t at $F_{pop} = 0.574$. Recent population fishing mortality values have been slightly above and below this value, and yield has

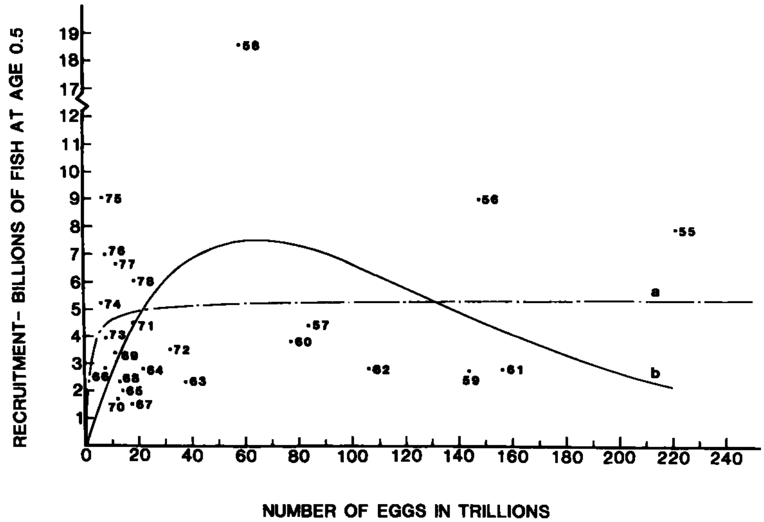

FIGURE 12.—Numbers of Atlantic menhaden recruits (R) in millions plotted against estimated egg production (P) in trillions for year classes 1955-1978. Curve a represents the fitted Beverton and Holt function, R = 1/(0.00019 + 0.00027/P). Curve b represents the fitted Ricker function, R = 325.35 P exp (−0.0158 P).

TABLE 8.—Estimates of Atlantic menhaden population size and catch in numbers in thousands (age 1 to maximum observed age), population exploitation rates, population *F*, and catch in thousands of metric tons, by year.

Year	Population size	Catch in numbers	Population exploit. rate (*U*)	Population *F*	Catch (t)
1955	6,955,987.3	2,357,430.0	0.3389	0.532	641.4
1956	8,305,282.6	3,528,450.0	0.4248	0.721	712.1
1957	9,829,843.1	3,212,090.0	0.3268	0.508	602.8
1958	7,125,101.7	2,613,150.0	0.3668	0.590	510.0
1959	17,630,370.1	5,342,240.0	0.3030	0.462	659.1
1960	9,309,904.0	2,702,940.0	0.2903	0.438	529.8
1961	6,843,711.6	2,598,060.0	0.3796	0.618	575.9
1962	4,587,482.6	2,048,280.0	0.4465	0.774	537.7
1963	3,602,666.4	1,667,620.0	0.4629	0.816	346.9
1964	2,770,398.2	1,426,470.0	0.5149	0.961	269.2
1965	2,593,453.3	1,260,362.0	0.4860	0.878	273.4
1966	2,127,951.0	991,157.0	0.4658	0.824	219.6
1967	2,592,784.2	977,255.0	0.3769	0.612	193.5
1968	2,098,231.9	993,717.0	0.4736	0.845	234.8
1969	2,281,471.7	710,048.0	0.3112	0.478	161.6
1970	3,507,601.0	1,379,039.0	0.3932	0.648	259.4
1971	2,555,012.9	896,250.0	0.3508	0.556	250.3
1972	4,466,635.5	1,664,286.0	0.3726	0.602	365.9
1973	4,294,409.0	1,780,916.0	0.4147	0.697	346.9
1974	4,433,007.7	1,671,675.0	0.3771	0.612	292.2
1975	5,401,009.0	1,857,415.0	0.3439	0.542	250.2
1976	8,927,821.9	3,005,106.0	0.3366	0.527	340.5
1977	8,652,084.7	3,181,191.0	0.3677	0.592	341.2
1978	7,855,446.4	2,622,620.0	0.3339	0.522	344.1
1979	7,370,472.2	2,353,757.0	0.3193	0.493	375.7

remained slightly below the MSY value (Fig. 13).

Catch and F_{pop} values were also fitted to a modified version of the Pella-Tomlinson (1969) model, which compensates for nonequilibrium conditions (PRODFIT)(Fox 1975), assuming two significant year classes. This technique resulted in an MSY estimate of 557,000 t at F_{pop} = 0.336 (Fig. 13).

The scatter plot of yield/F_{pop} contains three clusters of yield values: high abundance gears (1955-62), low abundance (high F_{pop}) years of 1963-68 (with the exception of 1967), and years of low to moderate population size (1969-79). These clusters are less distinct when yield is measured in numbers of fish rather than biomass. A Graham-Schaefer curve, fitted to fishing mortality and yield in numbers of fish, resulted in a numbers MSY of 2.383 billion fish at an optimum $F_{pop} = 0.522$ (Fig. 14). Each year's yield in numbers as compared to biomass (Fig. 13, 14) suggests that the fishery in the late 1970's was not produc-

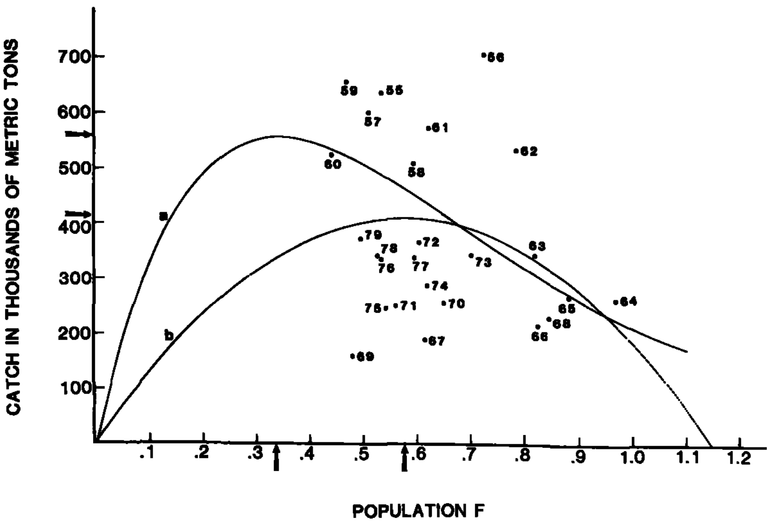

FIGURE 13.—Catch of Atlantic menhaden in thousands of metric tons plotted against estimates of population F for years 1955-79. Curve a is the result of fitting the Pella-Tomlinson's (1969) generalized yield function with adjustments for nonequilibrium conditions (PRODFIT, Fox (1975)). Curve b is a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

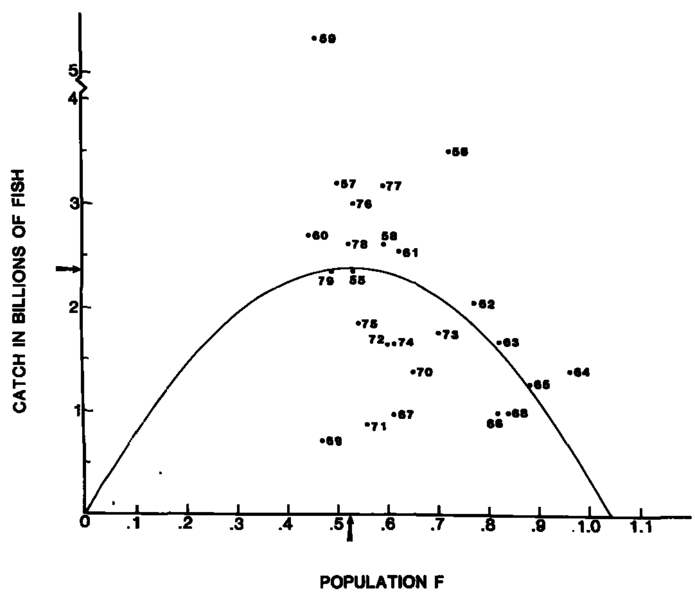

FIGURE 14.—Catch of Atlantic menhaden in billions of fish against estimates of population F for years 1955-79. The curve is the result of a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

ing the biomass in landings in proportion to numbers of fish caught when compared to earlier years.

Catchability coefficients (q_{pop}) for the population were estimated directly by dividing the F_{pop} estimates by nominal effort (vessel weeks) for years 1955-79. A plot of these estimates on population size indicates a pronounced inverse relationship similar to that shown by Schaaf (1975b), who estimated q differently (Fig. 15). Additionally, there is a pronounced historical trend in the data. There appear to be at least two families of points and thus two functional curves in the figure, 1955-69 and 1970-79. Beginning in 1959, the catchability coefficient progressively increased, the stock size was decreasing, and the fleet was becoming more efficient due to modernization and increased vessel size, coupled with technological innovations in the fishery operations themselves. This trend in efficiency probably made the ascent from the earlier, lower q_{pop} series of years exceptionally rapid. As population size began to increase after 1971, the catchability coefficient reflected a steady decline in magnitude, but it was at a level almost twice as great (hence a doubling in killing power or efficiency[7]) as from the late 1950's and early 1960's. Therefore, the reduction in the number of vessels from 1955 to the present did not represent a proportional reduction in potential effective fishing effort. In spite of the compounding effect of a true increase in efficiency (fishing technology), q, and thus F for given levels of effort, appear to be responding in inverse fashion to population size.

[7]Given modern day work weeks, real time spent fishing, and intervessel competition, the killing power has probably more than doubled.

The computed F_{pop} values are derived independently of nominal effort. Hence this set of values was used to determine if effort would be useful to verify trends in F at age or provide supportive information for improving the VPA estimates by employing more sophisticated models (see Deriso et al. 1985). A scatter diagram of the differences between estimates of F_{pop} and their mean on nominal effort demonstrated that no useful information is available from nominal effort when considering the entire time span involved (Fig. 16). The progressive increase in efficiency of the purse seine fleet, plus problems associated with estimating abundance with CPUE data from purse seine fisheries for schooling fishes (see Clark and Mangel 1979) makes nominal effort useful only for relatively short-time span comparisons between adjacent years, and then only when changes are pronounced.

Yield Per Recruit

Yield-per-recruit calculations for the 1970-78 fishing seasons were performed using the com-

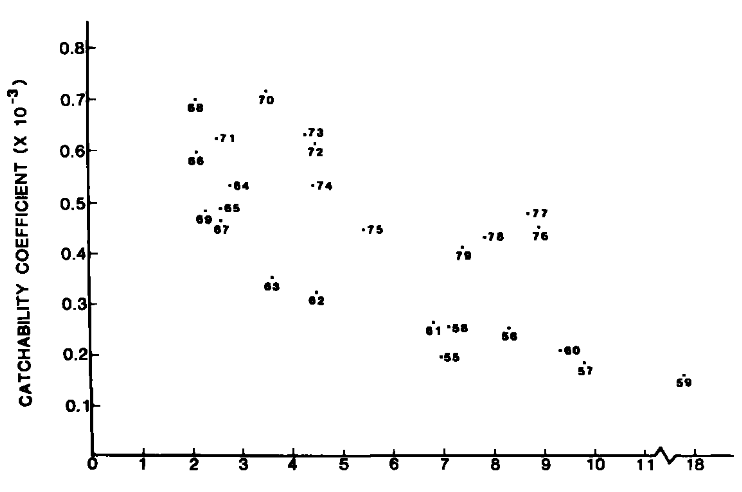

FIGURE 15.—Estimates of the Atlantic menhaden population catchability coefficient (q_{pop}) for years 1955-79, plotted against the estimated population size (excluding age-0 fish).

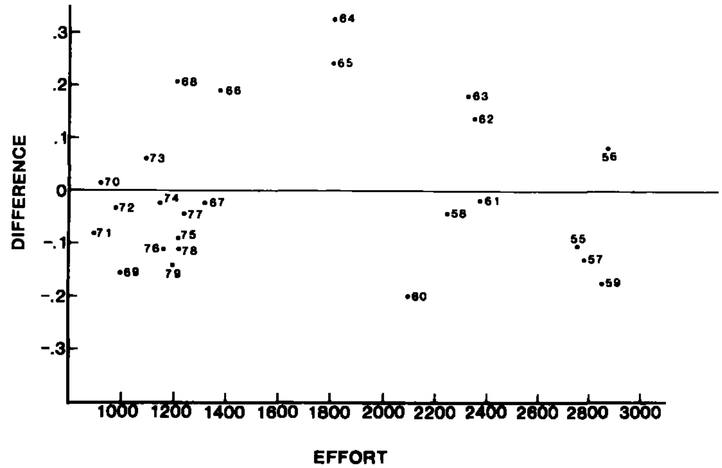

FIGURE 16.—Differences between observed Atlantic menhaden population fishing mortality rates (F_{pop}) and their mean plotted against nominal effort by fishing season.

puter program MAREA (Epperly et al. 1986) assuming exponential growth of the biomass in the population (Epperly and Nelson 1984). This program, modified for Atlantic menhaden from MGEAR (Lenarz et al. 1974), uses the Ricker-type yield-per-recruit model (Ricker 1975) and permits estimation of yield in each of the Atlantic menhaden fishing areas, with area-specific growth and fishing mortality rates. Each computer run of the model generates a matrix of yield per recruit at varied age of entry and multiples of F for each of the fishing areas (5) and one for the entire fishery. Yield for the entire fishery can be obtained either by summing yield from each area or by calculations based on input from the entire fishery estimated as a unit. A summation of the five matricies should be similar (but not equal) to the independently calculated entire fishery matrix. Input for the model includes estimates of area specific proportional fishing mortalities, estimates of weight at age by area and for the entire fishery, and an estimate of M (0.45).

Estimates of area-specific quarterly F at age were obtained by apportioning F at age for the entire fishery (obtained from the quarterly VPA, 1965-78 year classes) with the ratios of the number at age caught in a given area to the total number at age landed in the entire fishery. (The resulting proportional F's are not equivalent to true area specific F's, but are the correct values for the yield-per-recruit model used).

Area-specific length at age estimates for the beginning of each quarter for each year class were rearranged to correspond to fishing season, and converted to weight at age using season-specific weight-length equations (from Table 4). Parallel conversions were done on lengths at age for the entire fishery to estimate weights at age for the fishery as a whole.

Annual trends in historic yield per recruit were examined with the fishing mortality, age and size, and geographic pattern extant during each year from 1970 to 1978. Results from these computations indicate a severe decline in actual yield per recruit for the entire fishery and Chesapeake Bay area from 1971 to 1978 (Fig. 17).

Estimates of potential changes in yield per recruit under regimes of varied age at entry and (multiple) changes in fishing mortality rate were obtained by averaging parameters reflecting conditions during 3-yr intervals, i.e., 1970-72, 1973-75, and 1976-78 (Table 9). Attainment of the maximum potential yield from Atlantic menhaden in the purse seine fishery would have required a very high rate of fishing at a substantially delayed age at entry of about 3 years of age (Figs. 18, 19). More practically, yield could have been increased by reducing F's. For example, with a F multiplier of 0.6 and the current age of entry, the gain would have been 6.9% for the conditions of 1976-78 (Fig. 19, Table 9). With an increase in age of entry to 1.0 (eliminate the harvest of age-0 fish) the gain would have been 10.2%. The patterns of potential gain for conditions under the 1970-72 and 1973-75 time periods are similar, but of lesser magnitude (Fig. 18, Table 9).

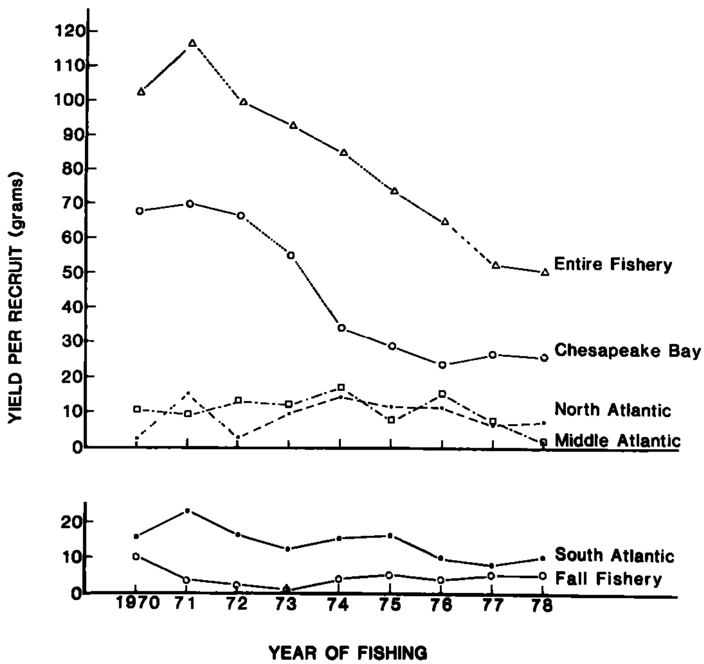

FIGURE 17.—Estimated yield per recruit of Atlantic menhaden for fishing patterns and growth prevalent during years 1970-78.

TABLE 9.—Estimates of percentage change in yield per recruit of Atlantic menhaden with varied age at entry and rates of *F* for 1970-72, 1973-75, and 1976-78. The *F* multiple of 1.0 represents the *F* at age vector extant during each of the three time periods.

Time period	Age at entry	*F* - multiple 0.4	0.6	0.8	1.0	1.2	1.4	1.6
1970-72	4.0	−35.8	−23.3	−16.1	−11.8	−9.2	−7.5	−6.3
	3.5	−21.9	−8.9	−1.7	2.6	5.3	7.3	8.7
	3.0	−12.7	0.2	6.2	9.8	12.0	13.4	14.4
	2.5	−4.6	6.8	12.1	14.9	16.5	17.5	18.1
	2.0	0.5	9.9	13.6	15.1	15.8	16.0	16.0
	1.5	−0.7	7.0	9.3	9.6	9.1	8.3	7.3
	1.0	−3.4	2.1	2.6	1.3	−0.6	−2.6	−4.7
	0.5	−3.9	1.4	1.5	(107.33)[1]	−2.1	−4.3	−6.5
1973-75	4.0	−7.7	4.6	10.5	13.6	15.4	16.5	17.3
	3.5	1.1	12.5	17.7	20.4	22.1	23.1	23.8
	3.0	10.5	20.2	24.2	26.2	27.3	27.9	28.4
	2.5	13.3	19.4	20.9	21.1	20.8	20.4	19.9
	2.0	12.8	15.2	14.8	14.0	13.2	12.5	12.0
	1.5	10.3	11.2	9.6	7.8	6.0	4.5	3.1
	1.0	8.2	8.1	5.6	2.9	0.5	−1.7	−3.7
	0.5	6.9	6.2	3.1	(84.07)[1]	−2.9	−5.5	−7.9
1976-78	4.0	−5.9	12.7	23.5	30.0	34.1	36.8	38.8
	3.5	1.5	18.8	27.8	32.7	35.5	37.1	38.1
	3.0	9.8	25.6	33.2	37.0	39.0	40.0	40.7
	2.5	12.1	22.7	26.0	26.5	26.0	25.1	24.2
	2.0	11.7	17.8	18.2	17.0	15.6	14.3	13.2
	1.5	9.6	14.0	13.2	11.0	8.8	6.7	4.9
	1.0	7.2	10.2	8.3	5.2	2.1	−0.7	−3.2
	0.5	5.0	6.9	3.9	(56.84)[1]	−3.8	−7.2	−10.3

[1]Estimated yield per recruit in grams for conditions of the time period, which is the base value for calculation of percentage change.

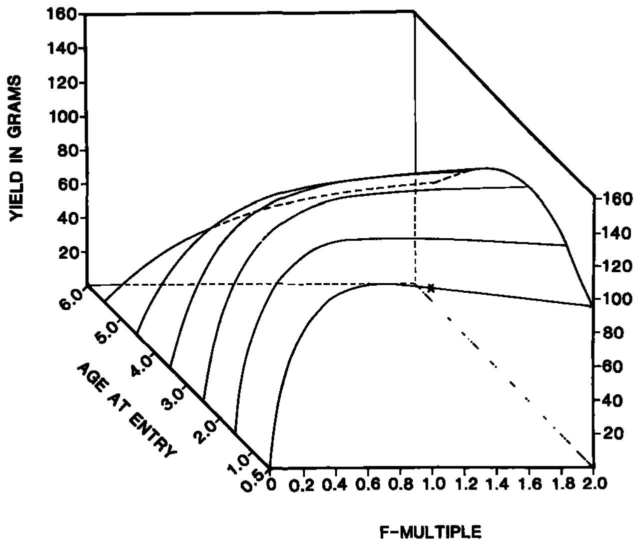

FIGURE 18.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for conditions extant during 1970-72. The X denotes estimate of actual yield per recruit for the time period.

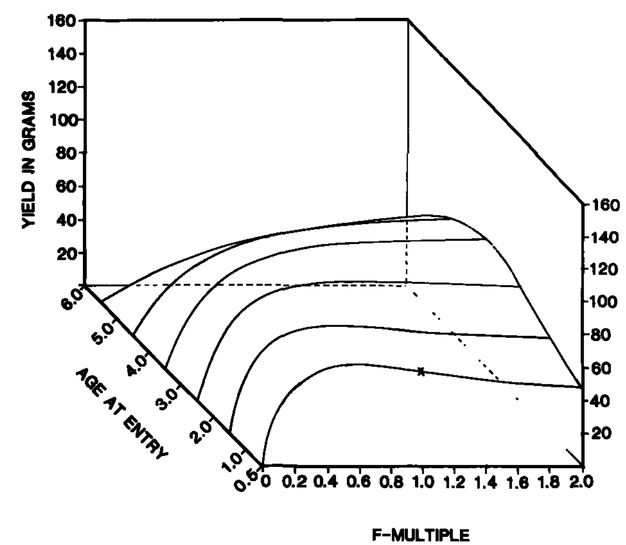

FIGURE 19.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for fishing conditions extant during 1976-78. The X denotes estimate of actual yield per recruit for the time period.

Results from these analyses indicate a general reduction in the maximum potential as well as actual yield per recruit from the early to the late 1970's, but the maximum potential total yield is greater in the later time period due to increased numbers of recruits (Table 10). Thus, estimation of potential changes in yield by the Atlantic menhaden fishery from yield-per-recruit models becomes a function of density-dependent growth rates (lower yield per recruit with larger year

TABLE 10.—Estimates of yield per recruit (grams) and mean yield (thousands of metric tons) of Atlantic menhaden for three, 3-yr intervals, maximum possible yield per recruit (Y/R) and yield with the existing fishing pattern.

Years	Mean no. of recruits $\times 10^6$	Estimated Y/R (g)	Mean yield estimate (t)	Maximum Y/R (g)	Maximum yield (t)	Increase %
1970-72	2,711.8	107.33	291.1	127.56	345.9	18.8
1973-75	3,778.2	84.07	317.6	108.40	409.6	29.0
1976-78	6,340.5	56.84	360.4	80.49	510.3	41.6

classes), rate of fishing, geographical pattern of fishing, age of recruitment, and numbers of recruits.

The general conclusion reached with these analyses is that the stock suffers from growth overfishing. To determine if a different initial choice of a constant rate of M would alter this conclusion, the relative biomass of a hypothetical year class was estimated at specific ages with M equal to 0.35, 0.45, and 0.55 and F equal to zero. The growth equation for the 1970 year class (from Table 3) and the annual weight-length expression for 1972 (from Table 4) were used in these computations. The age of maximum biomass decreases with increasing rates of M, as expected, but even at $M = 0.55$ the age of maximum biomass exceeds 2.5 years (Fig. 20). This decrease (from about age 2.8 for $M = 0.45$) is insufficient to affect the conclusion of growth overfishing. However, if the initial choice of M is too high, the analyses are underestimating potential gains in total yield that could be realized by decreasing fishing pressure on younger ages. Similarly, if the choice of M is too low, the analyses are overestimating potential gains, but a net gain would still be realized within the range of available estimates of M.

Actual Yield by Year Class

Using the estimates of numbers caught by age and annual weighted mean weights at age, annual landings were apportioned into biomass at age landed and then summed by year class through age 5. The calculations provide estimates of yield by each year class. A plot of yield against year-class size reveals lower than expected yields from the 1975 and 1976 year classes, given their magnitude (Fig. 21). This trend appears to have started about 1973.

Comparisons of growth and mortality patterns were made of similar-sized year classes, 1955 and 1976, and 1956 and 1975, in search of causes of the observed decrease in yield. Differences in fishing mortality rates at age do not explicitly account for the dramatic differences in yield between the two pairs of similar-sized year classes (Table 11). The 1955 year class was harvested at a greater (less desirable) rate during the critical

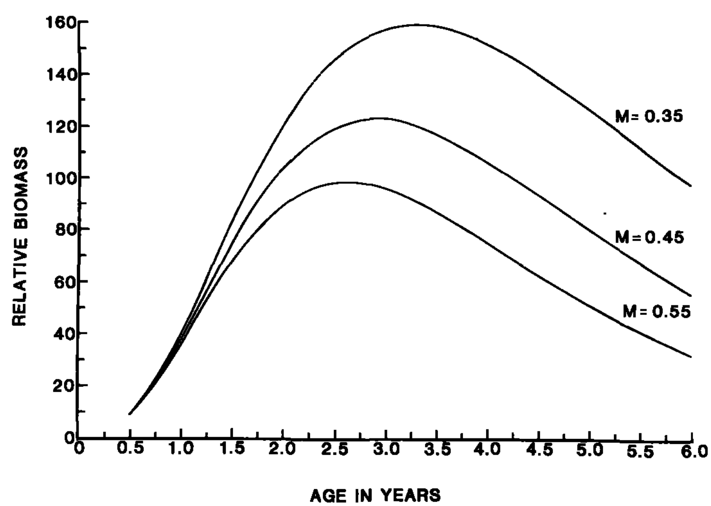

FIGURE 20.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, exposed to three rates of natural mortality. If the year class was harvested instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

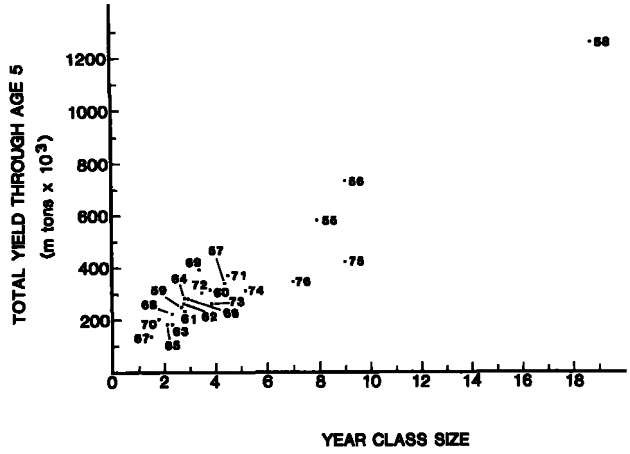

FIGURE 21.—Estimated yield contribution of Atlantic menhaden in thousands of metric tons, by the 1955-76 year classes through age 5, plotted against year class size.

TABLE 11.—Estimates of annual F at age for the 1955 and 1976, and 1956 and 1975 year classes of Atlantic menhaden, through age 5.

Year class	Age 0	1	2	3	4	5
1955	0.10	0.58	1.56	0.39	0.43	0.90
1976	0.04	0.27	1.51	0.57	1.04	1.02
1956	<0.01	0.32	0.88	0.74	0.61	0.48
1975	0.03	0.34	1.60	1.48	0.60	1.82

ages of 0-2 than was the 1976 year class. In fact, yield from the 1955 year class could have been markedly increased with a reduced fishing rate on these younger fish. The harvest rates of the 1956 and 1975 year classes were similar for ages 0-1, but markedly greater at age 2 for the 1975 cohort. While the high age-2 fishing mortality rate probably contributed to the lower yield, it did not fully explain the marked difference. The generally higher rates of F for ages 3-5 exhibited for both the 1975 and 1976 year classes were probably inconsequential for this comparison of yield.

While an increase in the true value of natural mortality could cause a decrease in total yield by year class, differences in growth provide a more obvious explanation for the differences within these two pairs of year classes. Growth curves (in length and weight) for the 1956 and 1975 year classes and the 1955 and 1976 year classes show that individuals were much smaller during the dominant harvest ages (1-3) for the two most recent year classes (Figs. 22, 23). These differences could be great enough to account for most of the differences observed in yield. Slower relative growth in post age-1 fish has been apparent for year classes 1973-78.

To determine if age of maximum theoretical biomass had changed owing to the different (flatter) shaped growth curves displayed by the year classes in the later 1970's, the relative biomass at age of an unfished hypothetical year class was estimated with the growth equation for the 1975 year class with M equal to 0.45 and the annual weight-length expression for 1972. The results display an increase in maximum age (to about 3.25 years), a decrease in total biomass, and a much slower ascent and even slower descent from maximum biomass than results for the 1970 year class growth curve (Fig. 24). These results indicate that age of entry to the fishery could have been greatly delayed in the later 1970's with little chance of losing yield.

Given the progressive decrease in average size at age of fish in the age classes which dominate landings (Fig. 25), the decline in yield per recruit following 1971 (Fig. 17) is expected. However, the rapid decline in size at age is not entirely ascribable to density-dependent growth. More importantly, the potential for increased yield with reductions in F is probably greater than the results from the MAREA yield-per-recruit model indicate owing to the likelihood of size selective fishing and the potential for differential stock-specific growth rates. Additionally, the relatively high MSY estimate obtained from the PRODFIT

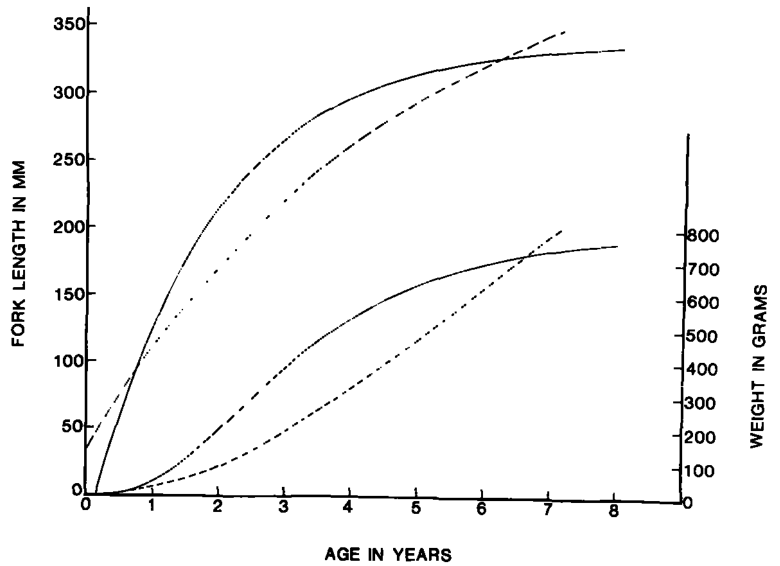

FIGURE 22.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1955 (solid curves) and 1976 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

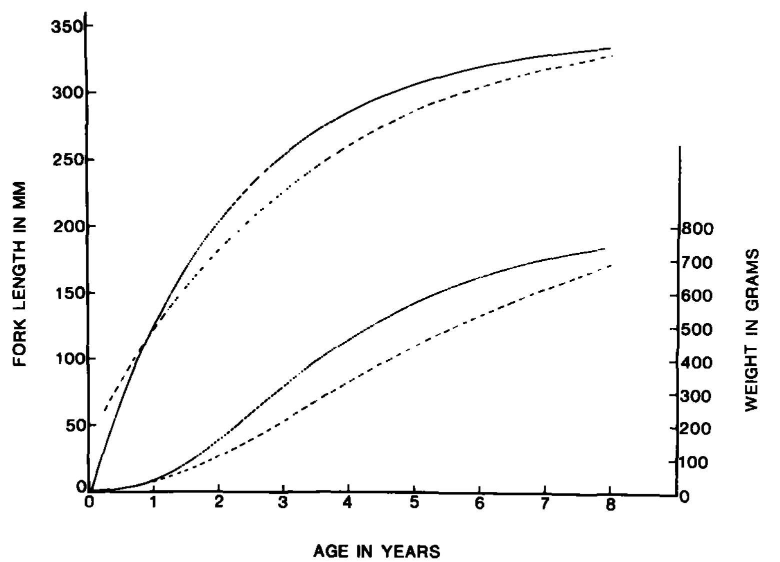

FIGURE 23.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1956 (solid curves) and 1975 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

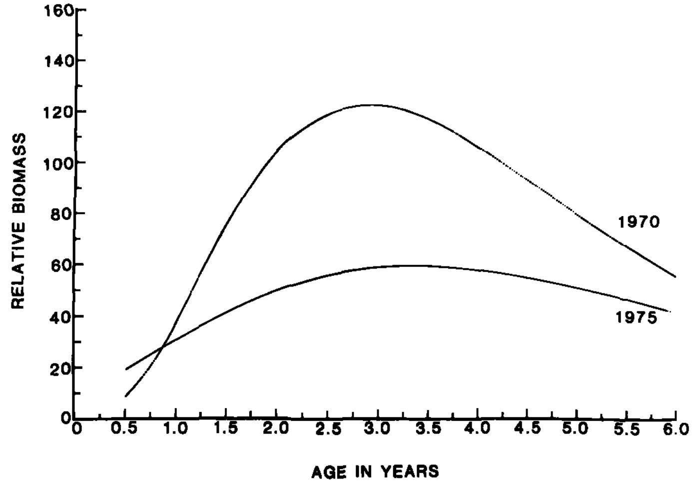

FIGURE 24.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, with growth parameters estimated for the 1970 and 1975 year classes. If harvesting occurred instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

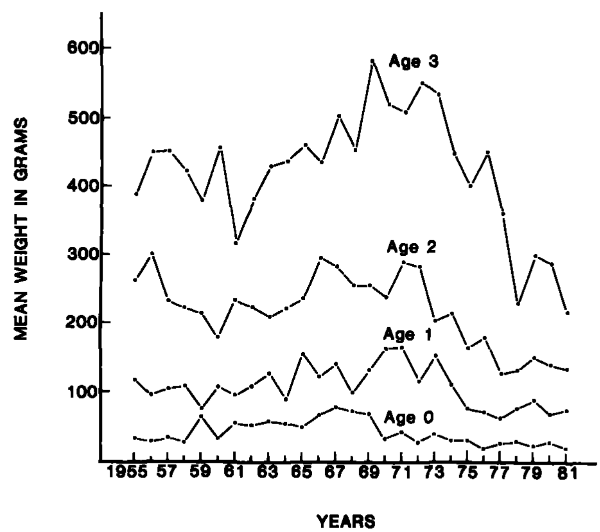

FIGURE 25.—Weighted mean annual weight of purse seine landed Atlantic menhaden, ages 0-3, for years 1955-81.

solution shown earlier may be more realistic than first impressions would indicate. However, to attain that level of harvest would require a restructuring of the fishery, and continued moderate to high levels of recruitment to sustain it.

GENERAL DISCUSSION

With estimates of year-class sizes, exploitation rates, and an understanding of the interaction of population size and effort relative to rates of fishing mortality, the trends observed in the fishery since 1955 are more readily explained. Additionally, this information permits inferences to be drawn about the earlier presampling period of the 1940's and early 1950's. The major premise of this discussion is that harvest levels and effort of the earlier presampling period were probably near the maximum that the population could support, and thus the rather rapid growth of the fishery in the early to mid-1950's was a response to a substantial increase in abundance of Atlantic menhaden and not simply increased effort applied to an underexploited stock.

Changes in stock abundance due to fluctuations in spawning success were prevalent in the 1940's. This conclusion is drawn from the statement of purpose for study given by June and Reintjes (1959). They noted changes in abundance among geographic areas and seasons and some poor catches. This condition is expected when recruitment fluctuates in a fishery that has a stock which is differentially distributed by age and size.

Data from early years indicated a limited resource. Catch closely paralleled effort for the 1941-47 seasons, but catches during 1948 and 1949 (about 350,000 t) were less than expected given the effort expended (Fig. 1). Apparently the stock subsequently underwent a marked increase in abundance, noticeable first about 1952, but even more pronounced in 1953 and 1954. The fishery responded, as effort again began to rise, but lagged for the next two or three seasons. In 1959 catches were dominated by the 1958 year class, which continued to provide significant biomass to the fishery through 1962.

It appears that the 1950's marked a period with above average recruitment, and this was accentuated with the apparently very large 1951 year class, followed by the three relatively large year classes of 1953, 1955, and 1956, and finally the largest documented year class of 1958. Recruitment did not return to the level of the 1955 year class (the lesser of the three documented large year classes) until 1975. To obtain some idea of relative sizes, a reconstruction of these earlier year classes was made using arbitrary, but conservative values for F (F = 0.25 for age 1 and 0.50 for age 2+) (Table 12). Given the (older) larger sized fish which were taken during the peak landing years, these speculative year class estimates are less than or nearly equal to a size necessary to support the large catches of the mid-1950's (see Figure 14 and Table 7).

The age structure of the Atlantic menhaden population has undergone at least two periods of expansion and contraction since about 1950, and has shown signs of expanding again by 1980 (Fig. 6). Inferences on early age composition were derived primarily from the early 1952-54 sampling of the fishery in the middle Atlantic area (June and Reintjes 1959, their appendix table 2). Age-5 and older fish were 1.0%, 0.8%, and 1.1% by number in the samples from that area for 1952, 1953, and 1954 as compared to 1.8% and 2.9% for 1955 and 1956. The 1951 year class dominated the catch during this period, comprising 84.59% of the samples as age 1, 98.05% as age 2, and 59.02% as age 3 in the middle Atlantic area and 87.11% as age 3 in the newly sampled north Atlantic area. Hence, as noted earlier, the stock probably had its strongest age structure in 1955 and 1956, which were coincidentally the first years for which port sampling covered the full geographic range of the fishery. This strength was due to the increased population size, subsequent decrease in the catchability coefficient, and thus a reduced fishing mortality on most age groups. Higher rates of survival led to more individuals in the older age groups. The landings were sustained above 500,000 t in the mid-1950's by contributions of the 1955 and 1956 year classes, but these year classes were too small to prevent an increase in mortality because of increased effort and the number of older fish were reduced by 1959. The large 1958 year class aided the replenishment of the older age groups, by about 1960. Without another large year class,

TABLE 12.—Estimates from virtual population analyses (mixed time interval, see text) of number at age in thousands on 1 March for the 1950-59 year classes of Atlantic menhaden. Bracketed values represent estimates obtained from back calculations using arbitrary values of F (0.25 for age 1 and 0.50 for ages 2+)

	Year class									
Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
1	[3,943,235]	[10,782,529]	[3,162,907]	[4,504,191]	3,040,558	5,621,258	7,153,549	3,263,196	14,767,294	2,164,428
2	[1,958,152]	[5,354,445]	[1,570,653]	2,236,715	1,410,646	1,976,767	3,306,709	1,412,179	6,627,079	1,158,337
3	[757,298]	[2,070,784]	607,436	642,482	240,748	274,476	893,865	275,897	2,357,641	361,743
4	[292,878]	800,857	189,410	169,952	80,038	119,036	270,347	116,411	602,146	71,280
5	113,268	281,543	86,255	53,482	37,304	48,835	92,494	59,258	75,460	11,589
6	43,677	63,025	23,309	21,243	14,284	12,269	35,962	14,698	8,894	1,616
7	5,980	11,726	7,639	3,717	2,765	5,618	4,883	1,629	901	161
[1]8	600	3,564	1,446	478	1,162	1,331	640	92	48	—

[1]This age group may contain a small number of age 9 or 10 individuals, see text.

mortality apparently again increased, as the age structure became markedly constricted by 1965, and drastically truncated by 1967. Recruitment began to improve by 1971, culminating with relatively large year classes in 1975 and 1979. Mortality rates for some ages began to decline during the late 1970's, and the older age groups began to strengthen, consistent with the decline of the catchability coefficient with increased population size.

With respect to yield per recruit, there appears to be no recorded period of Atlantic menhaden fishing when an ideal harvesting regime existed in the purse seine fishery. Age-0 fish have been harvested since at least 1955 (Figs. 8, 9). Except for influences of the exceptionally large 1951 and 1958 year classes, most of the catches sampled for age have been dominated by age 2 relative to biomass, and ages 1 and 2 relative to numbers. Major numerical but minor biomass contributions have been evident for age-0 fish. Inferences of the fishery's high dependency on younger age groups can be traced back to 1940. Given that the population distributes itself by age and size along the Atlantic coast, the quantity of landings and degree of effort expended in areas where younger and smaller fish predominate suggests a similar age composition for total catches during the presampling period (Figs. 3, 5).

Landings in the middle Atlantic area dominated the fishery in earlier years, but a shift had occurred by 1964, at which time Chesapeake Bay landings began to dominate (Fig. 4). Responding to a reduced population of larger and older fish, the industry increased the proportion of fishing effort exerted in areas closer to the large nursery areas of Chesapeake Bay and the south Atlantic area. Further, the fishery shifted from one that harvested the larger age 1's and 2's, and older fish, to one that harvests the smaller and younger fish. The larger, older fish were and still are vulnerable to the fishery during their fall migrations, but effort on these fish appears to be reduced within the north Atlantic and middle Atlantic areas.

A comparison of age-specific estimates of exploitation rates supports the earlier discussion on age dependency, population sizes, and age structure (Fig. 26). In the mid-1950's, the exploitation rates, although varying, were lower than those

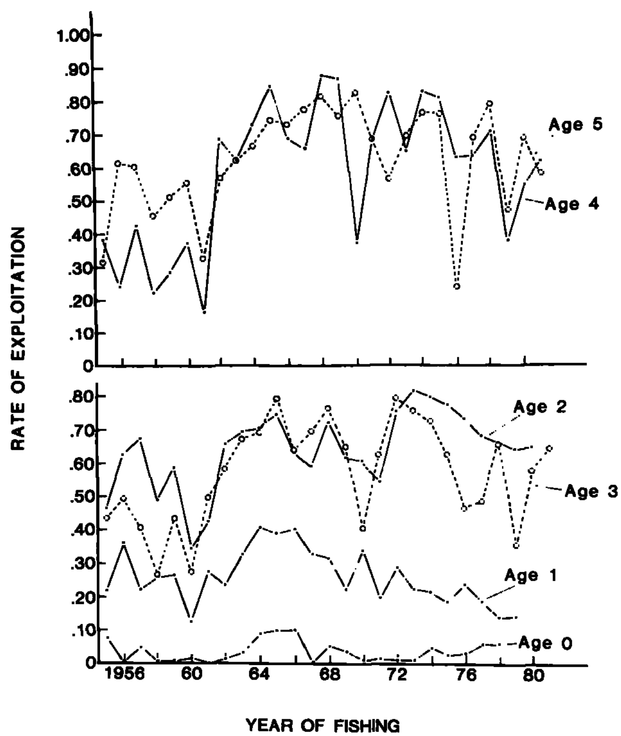

FIGURE 26.—Estimates of annual rates of exploitation of Atlantic menhaden, ages 0 through 5.

for the subsequent years when population size was decreasing. The rates reached their lowest points for ages 1-3 during 1960, when the 1958 year class was fully recruited. A low point followed for ages 4 and 5 during 1961. All exploitation rates generally increased during the low recruitment years of the 1960's, and began decreasing during the 1970's as the population size began to increase due to higher recruitment. The rate of reduction noted for nominal effort (Fig. 1) lagged behind that of the stock and was apparently too slow to prevent the observed rise in exploitation rates during the 1960's.

The exploitation rates of age-2 fish appear to have progressively declined during the later 1970's, following a disproportionately large increase after 1971. This increase apparently was a product of a shift in the pattern of fishing that occurred during the regrowth of the fishery and that pattern still exists. Although slightly lagging behind that of the age-2 fish, exploitation rates on age-0 fish began increasing by 1974, and reached an alarming rate of about 15% in 1979 (preliminary estimate). This rate of exploitation occurred in virtually one quarter of fishing and slightly exceeded the rate of exploitation for age-1 fish for the entire season. The disproportionately low exploitation rate on age 1's is probably due to their increasingly smaller size, a consequence of which would be a more southerly distribution. Additionally, many would remain in or near estuarine nursery areas and surrounding smaller bays and sounds, and thus be less available to the fishery.

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