LARVAL TRANSPORT AND YEAR-CLASS STRENGTH OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*[1]

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ABSTRACT

A Ricker spawner-recruit model was developed for Atlantic menhaden, *Brevoortia tyrannus*, from data on the 1955-70 year classes. The number of eggs produced by the spawning stock was calculated as the independent variable to account for changes in fecundity due to changes in population size and age structure. A survival index was developed from deviations around the Ricker curve and was regressed on several environmental parameters to determine their density-independent effects. The recruit-environment model accounted for over 84% of the variation in the survival index. Zonal Ekman transport, which acts as a mechanism to transport larval menhaden from offshore spawning areas to inshore nursery grounds, was the most significant parameter tested. Ricker functions for good and poor environmental years were developed, indicating the wide range of recruitment that can be expected at different stock sizes. Comparisons of spawner-recruit relations for Pacific sardine and Atlantic menhaden indicated striking similarities. Surplus yield for the Atlantic menhaden fishery was calculated from observed and predicted survival, and compared with the actual performance of the fishery.

One of the more intriguing and important problems in fishery science, that of the relative influence of spawning stock size and environmental variation on year-class strength, has resulted in a long-standing controversy among fishery biologists. The two principal reasons for investigating the effects of stock size and environmental change on year-class strength are, of course, to understand what has happened and to predict what will happen. Since environmental conditions will produce varying recruitment at a given stock size, one must determine both the reproductive potential under average environmental conditions, i.e., the density-dependent spawner-recruit curve, and the effect of varying environmental conditions, or the density-independent function. The difficulty comes, as Clark and Marr (1955) point out, in separating the relative influences of the two functions. A prerequisite for such an attempt is a reliable long-term series of data, adequate to estimate the size of the spawning stocks, the number of recruits, the age structure of the populations, the patterns of environmental variation, and the rate at which the resource is being harvested.

Biologists are in general agreement that the most critical survival period for many marine fishes is during the time of egg and larval drift. Major factors affecting survival during this period are food (Cushing 1969), cannibalism by filter-feeding parents (Radovich 1962; Murphy 1967), and ocean currents (Sette 1943). The first two of these factors are density dependent and tend to control population growth. Transport by ocean currents to or from areas favorable to survival is density independent and has been used to explain successful year classes of Atlantic mackerel by Sette (1943) and Atlantic haddock by Walford (1938). A relationship between winds and year-class success for the East Anglian herring fishery was reported by Carruthers (1938). Cushing (1969) pointed out that ". . . correlations between recruitment and winds were often successful for a period of years, after which they failed catastrophically."

Other density-independent factors, such as temperature, particularly in the sense of long-term climatic change, have been related to changes in spawning success and location. For example, a change in the environment of the Pacific sardine over a period of time which resulted in a change in normal distribution patterns and a series of poor year classes was postulated by Radovich (1962). Sissenwine (1974) documented a significant relationship between atmospheric temperature and the recruitment and equilibrium catch of yellowtail flounder, but did not explain

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the mechanism by which temperature anomalies influence the fishery.

Cushing (1969) listed three sources of variation which might affect recruitment: year-to-year environmental changes, larger scale climatic changes, and differences due to stock density. The year-to-year effects were considered by Cushing to be randomly distributed around the stock and recruitment curve and not of major consequence in the long-term regulation of fisheries. Over a number of years, variations around a stock and recruitment curve may tend to cancel one another and the fishery may provide a relatively stable yield. However, when a fishery is overexploited and subjected to poor survival as a result of environmental conditions, stock size may be reduced to a small fraction of that necessary to maintain a maximum sustainable yield (MSY). Further, with overcapitalization, fishing effort may remain high, preventing a resurgence of the stocks by maintaining a spawning stock too small to produce a large year class under favorable environmental conditions. From this standpoint, a predictive capability, based on knowledge of density-dependent and density-independent recruitment could be vital to the maintenance of adequate stock size through a reduction in effort, or to the harvesting of surplus population beyond that necessary to maintain the MSY. Fisheries, in the generic sense, operate over long periods of time. Fishermen, fish processors, and consumers operate on a much shorter time scale and large, unexpected, year-to-year fluctuations in stock size have significant economic and social impact.

The Atlantic menhaden, *Brevoortia tyrannus*, is a species that has supported a significant fishery since the middle of the 19th century (Reintjes 1969). Landings from the fishery have been sampled extensively since 1955 and the major characteristics of the stocks and the fishery have been determined. Information for a variety of stock sizes and from a range of environmentally different years is available, and the stocks have been subjected to heavy fishing pressure (Schaaf and Huntsman 1972).

A study of forecasting methods and the development of a forecast for the Atlantic menhaden fishery was carried out by the National Marine Fisheries Service (Schaaf et al.[4]). The manuscript points out that knowledge of the biology of recruitment of the Atlantic menhaden is needed to take advantage of strong year classes through the development of short-term fishing strategies. Knowledge of poor year classes would also be beneficial from a standpoint of avoiding excessive fishing pressure on the stocks.

A single year class is harvested by industry over a 4- to 5-yr period, and its failure could be masked to some extent by overfishing of other year classes taken concurrently, resulting in serious stock depletion. Conversely, a large year class may lead to a large increase in fishing effort which continues after the year class has been harvested, leading to overcapitalization and overfishing in subsequent years of reduced stock size. A large year class, followed by several poor year classes is potentially disastrous to the fishing industry and to the stocks. Knowledge of the recruitment process and the ability to predict year-class strength is necessary if the fishery is to operate at the MSY level.

Detailed information on the composition of Atlantic menhaden stocks obtained yearly since 1955 shows a range in numbers recruited into the fishery of from 11.5 billion in 1958 to 0.9 billion in 1967. Although some of the variation in recruitment can be attributed to fluctuations in the size of the spawning stock (Schaaf and Huntsman 1972), the wide range of fluctuations between years with similar spawning stock sizes suggests that environmental factors are influencing the survival of prerecruits. This study attempts to identify those factors, determine their relative influences, and develop a predictive model to account for the variations between actual and expected recruitment into the Atlantic menhaden fishery.

SPAWNING AND LARVAL DISTRIBUTION

Gravid or running-ripe Atlantic menhaden are rarely caught and spawning has not been observed. Without conclusive information, the time and place of spawning has been inferred by the relative ripeness of maturing ova, the occurrence of partially spent ovaries, and the distribution and occurrence of eggs and small larvae.

Higham and Nicholson (1964:262) reported that

[4]Schaaf, W. E., J. E. Sykes, and R. B. Chapoton. 1973. Forecast of 1973 Atlantic and Gulf menhaden catches based on the historical relation of catch and fishing effort. Unpubl. manuscr., 22 p.

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". . . (only 11 specimens containing numerous ripe ova were encountered in the routine field examination of several hundred thousand fish during 4 years of sampling), ..." Based on a sample of approximately 37,000 female menhaden from all Atlantic coast fishing areas, they concluded, p. 270, "Spawning apparently occurred in the North Atlantic Area [north of Long Island] from May to September; in the Middle Atlantic [south to Cape Hatteras], from March through May and again in September and October; and in the South Atlantic [south of Cape Hatteras], from October through March." Based on the percentages of sexually active (ripening but not ripe) females in their samples, it appears that a majority of spawning activities take place in the South Atlantic Bight. The spawning cycle appears to be one of limited spawning during a spring northward migration, limited early and late summer spawning as far north as Cape Cod and occasionally into the Gulf of Maine, increased spawning activity during a southward fall migration, and intensive (90-100% sexually active) winter spawning in the South Atlantic Bight.

Spawning activities through the winter are difficult to determine because the stocks move offshore and there is no fishery for menhaden during that period. This is the only time during the year that menhaden schools are not available in coastal waters, and that fact leads to speculation about an offshore spawning migration.

Available information about the distribution of menhaden eggs and larvae has been reviewed by Kendall and Reintjes (1975) and Chapoton.[5] Inferences regarding spawning activities have been drawn from various surveys of restricted time and coverage which have been conducted on the east coast since 1937 (Permutter 1939), primarily in sounds, bays, and creeks. Only two egg and larval research efforts have provided large-scale systematic coverage of major menhaden spawning areas on the Atlantic coast. Those are the cruises of the MV *Theodore N. Gill* (Reintjes 1961) and the RV *Dolphin* (Kendall and Reintjes 1975). The distribution of larvae collected by the *Dolphin* cruises is in general agreement with the spawning cycle documented by Higham and Nicholson (1964). RV *Dolphin* cruises covered the entire continental shelf from Cape Lookout, N.C., to Martha's Vineyard, Mass., in 14 transects from December 1965 to May 1966.

The southern part of the menhaden spawning range was covered by cruises of the *Theodore N. Gill* in 1953 and 1954 (Reintjes 1961). The absence of menhaden larvae during all but the winter cruises led Reintjes to conclude that menhaden spawn along the south Atlantic coast generally from December to February. The southern limit of the spawning range of the Atlantic menhaden is undetermined because a southerly species, the yellowfin menhaden, *Brevoortia smithi,* has an overlapping spawning range. Those larvae collected by the *Theodore N. Gill* off southern Florida were probably *B. smithi* and those collected off Cape Lookout, the other area of larval concentration located by the *Theodore N. Gill,* were undoubtedly *B. tyrannus.* Based on the distribution of juveniles and adults, it seems safe to assume that Atlantic menhaden spawn as far south as northern Florida, but at a low intensity in the extreme southern part of their range. Reintjes (1969) hypothesized that much of the spawning takes place south of Cape Hatteras.

Atlantic menhaden appear to spawn over most of the continental shelf. The general timing sequence and location of spawning during migrations indicates that eggs and larvae are subjected to an open ocean environment for a sufficient length of time to be affected by oceanic conditions. Both the *Dolphin* and *Theodore N. Gill* cruises resulted in catches of small larvae from nearshore to the edge of the shelf. *Dolphin* records show a general increase in average size of larvae from offshore to inshore stations as well as increased distance offshore from north to south. Major summer spawning in the New York-New England area appears to occur well inshore, and large numbers of eggs and larvae have been taken in bays and sounds from Long Island north. Matthiessen (1974) reported concentrations of eggs that exceeded 20,000/100 m^3 in June 1972 in Narragansett Bay, R.I., and computed the total production of eggs in the Bay during the summer of 1973 as being in excess of 4.64×10^{11}.

Concentrations of eggs and small larvae are found progressively nearer the offshore edge of the shelf during the fall and winter southward migration. Massmann et al. (1962) found larvae as small as 7 mm 79 km off Chesapeake Bay, and concluded that spawning and hatching occurred more than that distance offshore. Reintjes (1968) reported an extensive patch of menhaden eggs in Onslow Bay,

[5]Chapoton, R. B. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 69 p. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

N.C., in December 1966, 40 km from shore and estimated their age at 8 to 55 h. *Theodore N. Gill* cruises resulted in the location of larval menhaden up to 220 km off Cape Fear, N.C., in February 1954, although most larvae taken during the *Gill* cruises were over the shelf. Cruises of the RV *Undaunted* during the winter of 1970-71 also yielded larvae 170-175 km off Cape Fear.

PHYSICAL OCEANOGRAPHY OF THE SPAWNING REGION

An excellent summary of the oceanography of the coastal waters of the U.S. east coast was recently prepared by Bumpus (1973) and the reader is referred to that for detailed information. Bumpus identified three distinct subdivisions as the Gulf of Maine, Middle Atlantic Bight (Cape Cod to Cape Hatteras), and South Atlantic Bight (Cape Hatteras to Cape Canaveral). Although menhaden are periodically taken north of Cape Cod, Mass., migratory intrusions do not occur there routinely and the area is not one of significant menhaden spawning activity. A brief summary of oceanographic conditions in the other two regimes of significant menhaden spawning activities follows.

In the Middle Atlantic Bight the Gulf Stream diverges abruptly toward the northeast, passing Cape Hatteras, and the space between the Shelf Water masses and the Gulf Stream left by this divergence is occupied by the Slope Water mass. Flow in the Shelf Water and Slope Water is generally slow and southward, more or less parallel to the isobaths except for portions of the Slope Water mass near the Gulf Stream which have a northward to northeastward motion imparted by transfer of momentum from the Gulf Stream. At Cape Hatteras the southward flowing waters generally turn to flow northward and an unknown fraction of these waters becomes entrained within the Gulf Stream. The southward drift of Shelf Water is partly driven by the pressure field developed around river effluent plumes, and in times of low runoff and southeasterly winds the flow may be reversed. Menhaden spawning takes place throughout the Middle Atlantic Bight and oceanographic conditions there should have a major influence on the distribution and survival of eggs and larvae.

In the South Atlantic Bight the Gulf Stream current forms the seaward boundary of the region of intensive Atlantic menhaden spawning. The current's mean position is parallel to and a short distance (37-74 km in Carolina coastal waters) from the edge of the continental shelf (180-m isobath). A mass of Shelf Water which has lower salinity and lower temperature, except in summer, than the Gulf Stream water is found shoreward of the Gulf Stream. Motion of the Shelf Water mass is generally slow and variable, responding to local winds, but not customarily flowing southward, unlike the pattern of flow of the Shelf Water in the Middle Atlantic Bight. Occasionally southward flows have been identified near the coast, and the cuspate formations of Raleigh Bay, Onslow Bay, and Long Bay suggest southward flow nearshore as part of a large counterclockwise eddy in each bay. The existence of these eddies, although suspected, never has been conclusively demonstrated. Stefansson et al. (1971) found, based on geopotential topography from six cruises in 1966-67, that there was always an indication of a counterclockwise eddy in Onslow Bay. The pattern found in Raleigh Bay was less permanent and influenced by the influx of Virginian Coastal Water from the north.

LARVAL TRANSPORT

Menhaden larvae, spawned offshore, move into estuaries before metamorphosing to juveniles, after traversing long, open ocean distances. The larvae are 18-22 mm in length when they enter estuaries after an oceanic phase of 1½ to 2 mo. Very few small larvae (<12 mm) have been taken in estuaries along the central and southern U.S. Atlantic coast, even though eggs and young larvae have occasionally been taken near shore. The timimg of larval entrance is apparently controlled to some extent by the larvae and is somewhat independent of water movement. During earlier larval stages, however, there is a passive drift period in which larval movement is the result of ocean currents. Based on the rate of fin development, the completely passive phase probably ends when a length of 10-12 mm is reached. Depending on water temperature, menhaden reach that length in 30-45 days (William F. Hettler pers. commun., Atlantic Estuarine Fisheries Center).

Currents with an onshore component, particularly during the passive larval phase, would seem to be important for transportation of the larvae from offshore spawning areas to estuarine nursery grounds. There are no documented

physiological requirements for estuarine dependence, but metamorphosing larvae are rarely taken in the ocean, indicating that apparent requirements (food, shelter, etc.) provided by estuaries are essential in the life cycle of menhaden. Transport to the vicinity of estuaries should increase the opportunity for entering nursery grounds, resulting in good year classes from years of strong onshore transport. Weak onshore transport or water movement offshore would increase the distance that must be actively traversed, reduce chances of survival, and result in a poor year class. If variation in survival is due to variation in the efficiency of transport of larval menhaden from offshore areas to estuaries, then knowledge of the transport mechanisms would be useful for understanding and predicting variation in year-class strength.

Menhaden larvae have been found to be more abundant in the upper 15 m of the water column than in the underlying 18-33 m in extensive surveys of our Atlantic shelf waters (Kendall and Reintjes 1975; Chapoton see footnote 5). It is assumed, therefore, that they remain in the upper mixed layer and are transported along with it. Horizontal transport in the surface layer is principally the result of extensive quasi-steady-state currents and local, variable currents, which are strongly influenced by wind and run-off. Steady state currents, by definition, cannot be responsible for year-to-year variation in larval transport and recruitment, so attention was first turned to the local, variable currents which are superimposed on the quasi-steady-state circulation of the surface layer.

In the search for a westward transport mechanism which varies seasonally and from year-to-year, wind drift data computed from mean monthly atmospheric pressure distributions for the period 1946 to the present were considered first. In particular, plots of zonal (eastward or westward) wind-driven (Ekman) transport produced by the Pacific Environmental Group, NMFS, NOAA were studied (for method see Bakun 1973). A grid point (lat. 35°N, long. 75°W) located about 56 km southeast of Cape Hatteras was selected as being representative of the wind field in the area of interest. The seasonal variation of Ekman transport at lat. 35°N, long. 75°W generally includes relatively strong WSW-SW-SSW transport during the first quarter of each year. Because of the SW-NE trend of the coastline south of Cape Hatteras, Ekman transports significantly west of southwestward (those with a stronger westward component) would be most effective in transporting eggs and larvae toward estuarine nursery areas. Plots of the monthly zonal transport at this point revealed conditions of eastward or weak westward transport during most of the year, shifting to moderate or strong westward transport during January-March; a periodicity which matched that of spawning of menhaden south of Cape Hatteras (Figure 1).

In coastal waters of the Middle Atlantic Bight between Virginia and Long Island, N.Y., computations of monthly zonal Ekman transport exhibited a pattern similar to that found south of Cape Hatteras. Monthly zonal Ekman transport values computed for this area show that stronger westward transport generally occurs in the November-February period of menhaden spawning activities, possibly providing a mechanism for transporting menhaden larvae into the vicinity of estuarine environments.

A model of the circulation of the shelf waters off the Chesapeake Bight was developed and cited for its application to menhaden year-class strength by Harrison et al. (1967). The model was used in an attempt to explain the difference in "production of young menhaden" in Chesapeake Bay from the 1958 year class, an unusually productive one, and the 1964 year class, which was well below average. The model yielded inappropriate surface current regimes to explain strong shoreward larval transport in 1957-58, and Harrison et al. chose near-bottom currents, which appeared more favorable, as an explanation. As cited earlier, data collected in comparative net tows indicate that menhaden larvae are more abundant in the upper layer than the near-bottom layer, a condition which weakens the premise on which the argument is based.

Application of the Ekman drift data to the problem of explaining the large difference in menhaden production in Chesapeake Bay in 1958 and 1964 leads to a more satisfactory biological conclusion than the bottom-layer-transport model used by Harrison et al. (1967). The average monthly westward Ekman transports for the November-March period at two points in the Middle Atlantic Bight for 1957-58 (Table 1) were about twice as large as those for 1963-64, qualitatively implying that variation in wind-driven surface layer transport of larvae may be at least partly responsible for the amount of variation in menhaden year-class strength.

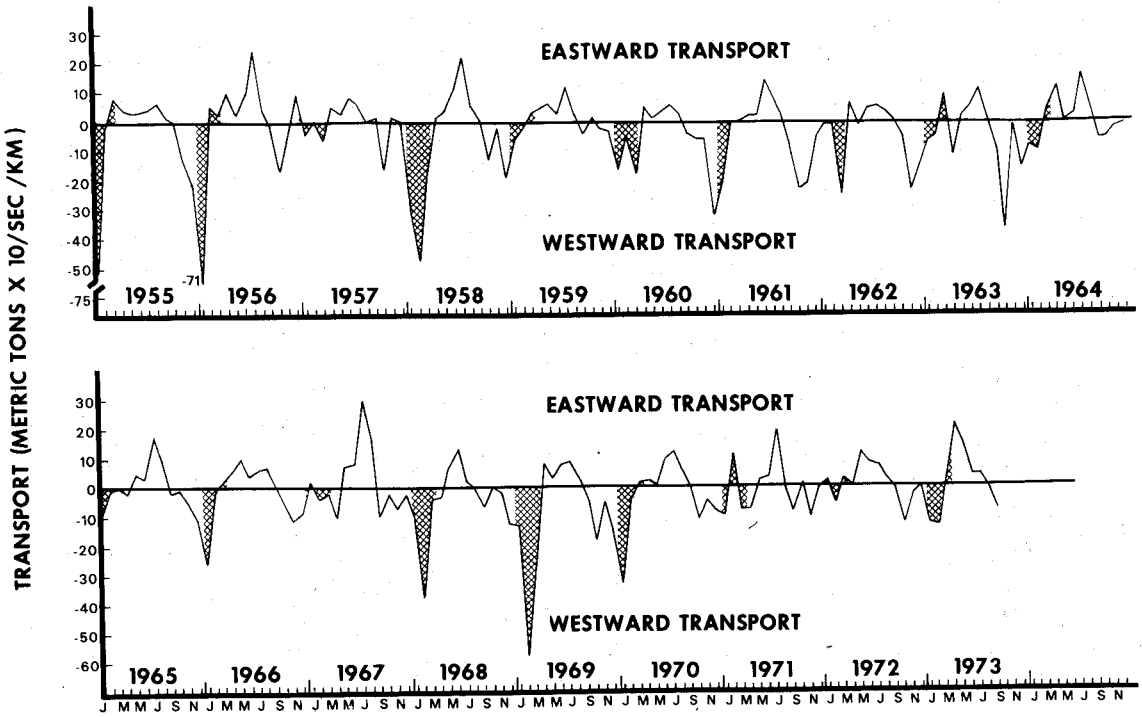

FIGURE 1.—Monthly average zonal Ekman transport at lat. 35°N. long. 75°W, 1955-73. January-March spawning period is shaded.

TABLE 1.—Average westward wind-driven Ekman transport computed for November-March 1957-58 and 1963-64 at lat. 39°N, long. 72°W and lat. 39°N, long. 75°W. Transports expressed in metric tons per second per kilometer of front.

Year	Lat. 39°N, long. 72°W	Lat. 39°N, long. 75°W
1957-58	480	520
1963-64	250	260

SPAWNER-RECRUIT RELATION

Over the 16 yr from 1955 to 1970, there was a sharp decline in the size of the Atlantic menhaden spawning stock and the size of resultant year classes. From 1964 to 1970, the annual catch of spawning age fish averaged only 14% of the previous 9 yr. Resultant per-year recruitment from 1964-70 averaged 42% of that for the previous 9 yr (Schaaf 1972). A description of the average relationship between spawning stock size and recruitment is useful for examining this coincident reduction and for predicting the expected fate of the fishery under different exploitation regimes. A stock-recruit function is also the necessary starting point for developing an index of survival (observed recruitment to that expected from number of spawners) against which one may assess the impact of density-independent environmental effects of recruitment. The approach in this study has been to determine if selected density-independent environmental factors could explain deviations from a postulated spawner-recruit model.

Ricker's (1954) comprehensive study of stock-recruitment formulated a dome-shaped model, with strong compensation, resulting in decreased recruitment at stock sizes beyond some maximum value. It is described by the equation:

$$R = Se^{(S_r - S)/S_m}$$

where R = recruitment
S = spawning stock
e = base of natural logarithm
S_r = maximum equilibrium stock
S_m = stock size yielding maximum absolute recruitment.

Ricker's model states that some stock size (S_m) produces maximum recruitment, and that, because of density-dependent mortality and growth,

stocks greater than S_m produce progressively fewer recruits. There is a size-dependent fecundity relationship for Atlantic menhaden (Higham and Nicholson 1964), and growth rates are slower for large year classes (Gene R. Huntsman, pers. commun., Atlantic Estuarine Fisheries Center). Also, adult menhaden are indiscriminate filter feeders and are known to ingest their own eggs. Calculation of a density-dependent index for Atlantic menhaden (i.e., the slope of a regression of $\ln R$ on $\ln S$) yields a value of 0.238. This index falls within the category described by Cushing (1971) as having a slightly convex spawner-recruit curve. The average fecundity of Atlantic menhaden (113,000 eggs per female) calculated from data used in this study, also places the species in groups which Cushing describes as having a dome-shaped spawner-recruit curve. Accordingly, the Ricker model has been used in this analysis, instead of models proposed by Beverton and Holt (1957), and others.

Schaaf and Huntsman (1972) presented a Ricker spawner-recruit curve for Atlantic menhaden. The same catch data and basically the same methodology were used in this study, with one important modification. Instead of using the estimated total number of spawning age fish as the independent variable to estimate recruitment, the potential number of eggs that could be produced from the spawning stock was used. This annual potential is influenced by the age distribution of the spawners and their average size. The potential number of eggs produced each year and at each age (Table 2) was calculated from the estimated number of age 3 and older females (1955-70), their back-calculated length, and the following fecundity relation from data presented by Higham and Nicholson (1964):

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

where E = thousands of eggs produced per female at length, and
l = back-calculated length at age of annulus formation for age-3 and older fish.

Another deviation from the data used on the original Ricker spawner-recruit curve by Schaaf and Huntsman (1972) is the calculated number of recruits in the 1955-70 year classes. The numbers differ between the two studies because: 1) some adult menhaden were reaged following the initial study which brought about slight changes in estimates of year-class size, 2) the maximum instantaneous fishing mortality rates were averaged for age-specific exploitation rates for age 2-5 fish and were not weighted for numbers at age as was done in the earlier study, and 3) the exploitation rate of age-1 fish was estimated each year based on the exploitation rate of age 2-5 fish instead of an estimated exploitation rate of two-thirds that of older fish as was done in the previous study. This was necessary because shifts in fishing area and effort in recent years have increased the vulnerability of age-1 fish.

The parameters of the Ricker model were estimated from a linear regression of $\ln(R/S)$ on S. Fitting the model (Figure 2) yielded an estimate of S_m equal to 60×10^{12} eggs. This is equivalent to 531 million spawning females spread over ages 3-6, and would produce an average recruitment of 3.68 billion fish at age 1.

TABLE 2.—Estimated number of eggs produced by spawning stock of Atlantic menhaden for each year class by age, 1955-70.

Year	Age 3	4	5	6	7	8+	Total
	Number of eggs $\times 10^{12}$						
1955	36.2	72.1	12.6	4.3	0.9	0.3	126.4
1956	45.7	11.1	52.8	12.5	3.4	1.1	126.6
1957	15.5	15.1	12.2	13.8	1.8	0.6	59.0
1958	11.4	6.3	6.8	4.9	3.0	0.3	32.7
1959	49.0	10.8	5.0	6.0	2.5	1.1	74.4
1960	18.1	36.8	12.6	4.7	1.7	0.5	74.4
1961	146.2	5.5	12.0	1.4	0.6	0.2	165.9
1962	23.9	56.7	7.2	6.4	0.9	0.2	95.3
1963	15.4	8.8	12.2	3.3	1.1	0.2	41.0
1964	8.5	3.8	1.9	2.1	0.5	0.1	16.9
1965	7.8	1.7	0.3	0.4	0.2	+	10.4
1966	3.9	0.9	0.1	+	0.1	+	5.0
1967	9.7	1.0	0.1	+			10.8
1968	6.7	2.0	0.2	+			8.9
1969	9.4	1.4	0.1	+			10.9
1970	7.7	2.9	0.2				10.8

+ = less than 0.05×10^{12}.

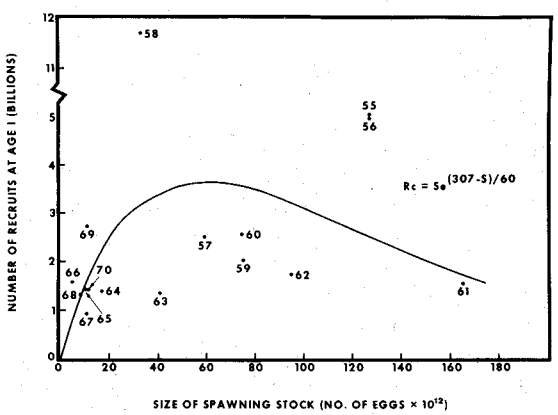

FIGURE 2.—Ricker spawner-recruit relationship for Atlantic menhaden, 1955-70.

Because the regression of $\ln(R/S)$ on S, as is done for the Ricker equation, will automatically give a significant correlation coefficient, a nonlinear fitting procedure was also applied to the data (Marquardt 1963). A comparison of the residual mean squares of the two procedures yielded an F of 1.02, indicating no significant difference in the fit of the Ricker curve to the spawner-recruit data between the standard technique and the nonlinear estimation.

Few published stock-recruitment curves appear to fit the observed data well, and the one for Atlantic menhaden is no exception. Application of a power function of the form $R = aS^b$ to the data resulted in a fit that was not significantly better from that of the Ricker function. The purpose of the study, however, is to examine and explain the deviations from the curve caused by density-independent factors, to see if they can be predicted, and consequently to improve upon a management plan based solely on a long-term, average MSY concept. The survival index (Table 3) represents the ratio of observed recruits (the number of age 1's in the population as estimated from the catch of age 1's and estimated exploitation rates) to the number calculated from the Ricker spawner-recruit model. This ratio is an index of survival, independent of density, and should reflect those environmental effects which influence survival of menhaden from the time of spawning until the time of recruitment to the fishery at age 1.

TABLE 3.—Estimated number of eggs, observed and expected number of recruits at age 1, and density-independent survival index for Atlantic menhaden, 1955-70.

Year class	No. of eggs $\times 10^{12}$	No. of observed recruits (R_O) $\times 10^6$	No. of expected recruits (R_C) $\times 10^6$	Survival index R_O/R_C
1955	126.4	5,019	2,569	1.95
1956	126.6	4,984	2,568	1.94
1957	56.0	2,538	3,688	0.69
1958	32.7	11,540	3,166	3.64
1959	74.4	2,007	3,599	0.56
1960	74.4	2,568	3,598	0.71
1961	165.9	1,553	1,751	0.89
1962	95.3	1,740	3,253	0.54
1963	41.0	1,378	3,457	0.40
1964	16.9	1,408	2,134	0.66
1965	10.4	1,406	1,472	0.96
1966	5.0	1,579	773	2.04
1967	10.8	922	1,505	0.61
1968	8.9	1,324	1,282	1.03
1969	10.9	2,763	1,521	1.82
1970	10.8	1,415	1,499	0.94

INFLUENCE OF EKMAN TRANSPORT AND OTHER FACTORS

The influence of transport processes in the southern part of the spawning range is indicated in Figure 3 which depicts the Ekman transport index for the January-March spawning period for 1955-70 and the estimated number of menhaden recruits at age 1 from the year class. The responsiveness of survival to transport shows up well in the Figure where years of strong westward transport correspond with large year classes, and weak transport years with smaller year-class size. Also, increases and decreases in recruitment from one year to the next generally coincide with an increase or decrease in westward transport in the year in which the year class was produced.

The correspondence is weaker in the 1968-70 year classes, although it follows the general pattern. Intense fishing pressure over a number of years changed the age structure of the spawning stocks to a considerable extent. For example, approximately 40% of the estimated spawning stock in 1958 were 4 yr or older. The number of age 4 and older fish in the 1969 spawning population was only about 9%, and the average number of eggs per spawning female was about 50,000 less than in 1958. Thus, fishing pressure brought about an even greater reduction in spawning potential than is apparent when considering the number of spawners alone, because of a reduction in the average age. This reduction in real spawning potential reduced the opportunity for a large-scale response to favorable transport in the 1968-70 year classes.

Comparison of the density-independent survival index with Ekman transport yields a surprisingly consistent relationship (Figure 4). A

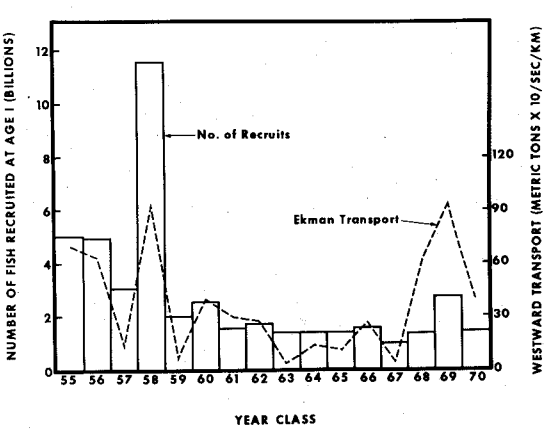

FIGURE 3.—Observed number of Atlantic menhaden recruits at age 1 and sum of average monthly zonal Ekman transport at lat. 35°N, long. 75°W for January-March of spawning years, 1955-70.

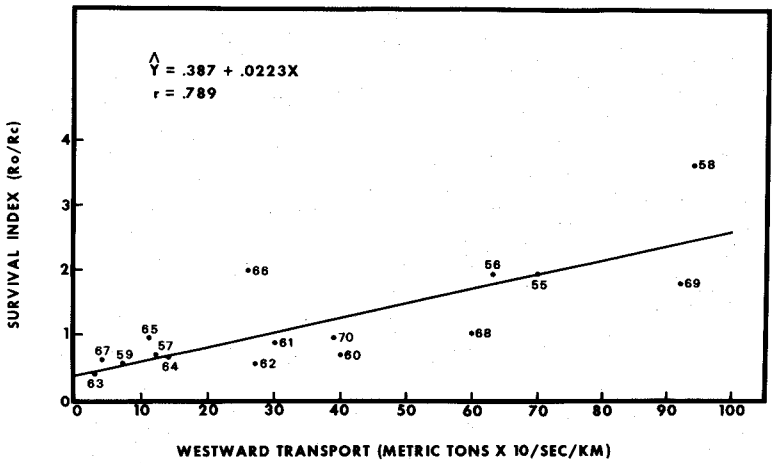

FIGURE 4.—Linear regression of calculated survival index (observed recruits/calculated recruits) for Atlantic menhaden on sum of January-March zonal Ekman transport at lat. 35°N, long. 75°W, 1955-70.

linear regression of survival indices against transport values for the January-March spawning periods at lat. 35°00′N and long. 75°00′W results in an r of 0.789 significant at the 0.001 level with 14 df (Figure 4). This accounts for approximately 62% ($r^2 = 0.622$) of the variation between observed and expected recruitment. Since the transport is indicative of conditions over only a portion of the total spawning range of Atlantic menhaden, and since r^2 accounts for such a large share of the total variation in overall recruitment, the actual effect of transport processes in the southern spawning area must be of overriding significance for the survival of spawn south of Cape Hatteras. With the exception of 1966, the index of survival was greater than 1.0 only when the Ekman transport index indicated a strong westward transport for the January-March period of menhaden spawning activities south of Cape Hatteras.

The transport data fall conveniently into groups of 0-200, 200-500, and 500-1,000 metric tons/s·km of ocean front. Five years of strong westward transport (>500) were found, and in all of these years the survival index was greater then 1.0. The observed recruitment exceeded the expected by an average of 108%, with the 1958 year class showing the largest value. In 6 yr of low westward transport (0-200), the survival index was never greater than 1.0: In 5 yr of moderate or "average" westward transport, (200-500) high survival occurred in 1 yr, and poor or moderate survival in the other 4 yr, indicating the influence of additional factors over the spawning range that are operating to produce variations in year-class strength. The high index for 1966 may partially result from the fact that the estimated spawning stock production of 5×10^{12} eggs was, by far, the lowest of any year on record (Table 2). Under such low stock size, density-dependent survival may have exceeded that indicated by the Ricker curve, creating an artificially high index of survival. A slight underestimation in the computation of the number of spawners would also create a very high survival index, since the slope of the Ricker curve is extremely steep as spawning stock size approaches zero (Figure 2).

Transport values at lat. 33°N, long. 78°W, approximately 200 nautical miles southwest of lat. 35°N, long. 75°W were also considered. The data are from a point offshore of Long Bay, S.C., the southernmost of the cuspate Carolina bays, and serves as an indicator of Ekman transport in the extreme southern part of the Atlantic menhaden spawning range. A significant correlation existed between transport for the January-March period and the survival index (Table 4). Due to the correlation between the two transport values south of Cape Hatteras, however, little additional variation is accounted for by the southernmost transport value (Table 5). Since transport is a function of wind stress and Coriolis force, movements of air masses through the southeastern United States would give parallel transport values at the two locations, with intensity of transport dependent on variations within the air mass. The large amount of variation accounted for by the two transport indices south of Cape Hatteras is sufficient to account for the relative success or failure of a year class, and supports the observation that a significant portion of menhaden spawning takes place south of Cape Hatteras.

TABLE 4.—Stepwise regression of survival index of Atlantic menhaden on environmental factors.

Factor	No.	Time of year	Correlation with survival index	Individual level of significance	Cumulative correlation	Error mean square	Cumulative percent of variance
Zonal Ekman transport lat. 35°N, long. 75°W	X_1	Jan.-Mar.	0.789	0.001	0.789	0.298	62.2
Chesapeake Bay discharge	X_6	July-Sept.	−0.216	—	0.825	0.271	68.0
Zonal Ekman transport lat. 39°N, long. 72°W	X_3	Nov.-Feb.	0.352	—	0.840	0.270	70.6
Zonal Ekman transport lat. 39°N, long. 75°W	X_4	Nov.-Feb.	0.519	0.05	0.896	0.198	80.3
Minimum temp Delaware Bay entrance	X_5	Jan.-Feb.	−0.177	—	0.914	0.181	83.6
Zonal Ekman transport lat. 33°N, long. 78°W	X_2	Jan.-Mar.	0.720	0.005	0.919	0.190	84.5

TABLE 5.—Regression coefficients between independent environmental variables used in the recruit-environment predictive equation for Atlantic menhaden. See description of X's in Table 4.

	X_2	X_3	X_4	X_5	X_6
X_1	0.789	0.645	0.644	−0.333	0.032
X_2		0.589	0.701	−0.580	−0.068
X_3			0.868	−0.403	0.174
X_4				−0.510	0.213
X_5					0.023

Wind-driven transport off Delaware Bay was studied as being representative of menhaden spawning areas in the Middle Atlantic Bight. Because the transport values are produced in a 3° grid by the Pacific Environmental Group, there were no available data for a point located centrally on the continental shelf. Two locations were chosen: one at lat. 39°N, long. 75°W, near the mouth of Delaware Bay, the other at lat. 39°N, long. 72°W, near the outer edge of the continental shelf. The two locations are approximately 260 km apart in an east-west direction, and are felt to be representative of Ekman transport over the broad shelf area near the east-west axis of the Middle Atlantic Bight.

The entrance of larvae into estuaries of the Middle Atlantic Bight occurs variably from September to June, with peak immigration occurring in the winter. Reintjes and Pacheco (1966) reported on 6 yr of larval collection at Indian River, Del., and showed high rates of influx from December through March. The peak month varied from year to year, but stayed within the December-March period. Correlation coefficients between summed transport values for November-February (the peak period of larval drift) and the survival index (Table 4) are not as large as those from south of Cape Hatteras, but the effect of transport on survival at the inshore point (lat. 39°N, long. 75°W) is significant at the 0.05 level. The transport values from the inshore and offshore points account for approximately 27% and 12%, respectively, of the total variance in the survival index for Atlantic menhaden. When combined with the transports south of Cape Hatteras, these values for the Middle Atlantic Bight account for an additional 12+% of the residual variance. Correlation coefficients are lower than those found for the South Atlantic Bight, and may be indicative of: 1) major nearshore spawning activities, reducing the need for a suitable transport mechanism; 2) a lower level of spawning in the area; or 3) a lower level of recruits per spawner due to mortalities from other environmental factors in the area.

The model of circulation off Chesapeake Bay developed by Harrison et al. (1967) and discussed in the Larval Transport section would be appropriate if larval menhaden were demersal in nature. However, since larvae are more abundant in the upper water column, we would expect a negative relationship between discharge and survival in the Middle Atlantic Bight because high surface discharge would impede larval entrance into estuaries. Chesapeake Bay was chosen to test that hypothesis because of its importance as a major nursery area. Average monthly discharge rates from the Susquehanna, Potomac, and James rivers were used in the test because they constitute over 90% of the total inflow into Chesapeake Bay. Discharge during the third quarter (July-September) of the year preceding the year-class year was chosen because there is a lag time of up to 90 days between stream flow and bay discharge (Harrison et al. 1967). The influence from run-off would be felt at the mouth of the Bay in the October-December period when larvae begin entering in increasing abundance. A correlation between the survival index and discharge rate did not result in a significant

coefficient (Table 4). When combined with the other factors considered above, Chesapeake Bay discharge accounts for an additional 6% of the residual variance in density-independent year-class strength. A fairer test of the effects of discharge on larval transport would require that we isolate that portion of the total larval production that would enter Chesapeake Bay under varying conditions. Our knowledge of Atlantic menhaden spawning activities is not sufficient to do this with reasonable precision.

An absence or reduction in the number of larvae in estuaries during periods of extreme cold has been noted by June and Chamberlin (1959) and Reintjes and Pacheco (1966). Kendall and Reintjes (1975) hypothesized that severe winters, particularly in the northern segment of the spawning range, result in heavy kills of overwintering larvae in the estuaries. In addition, laboratory acclimation studies have shown high mortality rates when menhaden larvae were held for several days at temperatures below 3°C (Lewis 1965). A time series of minimum mean monthly sea surface temperatures was located for the mouth of Delaware Bay from National Ocean Survey Tide Station Observer Records (U.S. Department of Commerce 1973). These data were considered representative of mid-to-northern coastal areas in the Middle Atlantic Bight. Correlation of the survival index for the entire population and the minimum temperature yielded a low correlation coefficient (Table 4). The correlation is somewhat of an artifact, however, and probably is biased by the positive correlation between Ekman transport and year-class strength. Westward Ekman transport is generated by winds from the north. Years of high westward transport in winter months are years of sustained north winds, which are associated with cold air masses. Under such conditions, we would expect cooler sea-surface temperatures in those years, particularly in or near shallow estuarine areas. There may be a positive correlation between temperature and survival, but the relationship probably is masked by the overriding effects of wind-generated Ekman transport (Table 5). The low correlation coefficient could also indicate that only a small portion of the population would overwinter in northern waters where temperature stress might be a significant factor.

If low temperature reduces survival, a transport mechanism to carry fall-spawned larvae southward along the Middle Atlantic Bight into the vicinity of estuaries that have milder winter temperatures would be a positive survival factor. Therefore, the meridional (north-south) component of Ekman transport in the Middle Atlantic Bight at lat. 39°N, long. 72°W near the edge of the shelf off Delaware Bay was considered. A correlation between the survival index and the southward transport for the October-December spawning period resulted in a coefficient of 0.336, which accounts for about 10% of the total variance in density-independent recruitment. However, the contribution to reduction in residual variance was minimal, because all of the variation due to southward transport was accounted for by linearly related east-west zonal Ekman components already considered. A relatively steady state southward transport mechanism exists in the Middle Atlantic Bight in the form of a southward flowing current over the shelf (Bumpus 1973). Because this current is quasi-permanent, variations in southward Ekman transport may be of little significance and may only create minor fluctuations in strength of an existing transport mechanism.

RECRUIT-ENVIRONMENTAL MODEL

The logic used in the selection of environmental parameters for inclusion in a model of environmental effects is depicted schematically in Figure 5. The heavy line represents an intuitive weight of density-dependent and density-independent factors in the survival of menhaden larvae from the time of spawning through their oceanic phase. In the upper Middle Atlantic Bight, for example, spawning takes place close to shore or in major bays and sounds, reducing or eliminating the time spent by larvae in the open ocean. This would reduce dependence on favorable currents for transport. Under such conditions, environmental factors influencing mortality may be relatively stable, with variation in the number of fish spawning in the area being the probable cause of most of the variation in the number of recruits produced. In the South Atlantic Bight, however, spawning takes place offshore, and dependence on favorable ocean currents would seem to have greater weight than spawning stock size on survival. Large annual variations in transport would produce large variations in survival in the South Atlantic Bight at a given stock size. The lower Middle Atlantic Bight seems to be an intergrade between the two extremes, with sig-

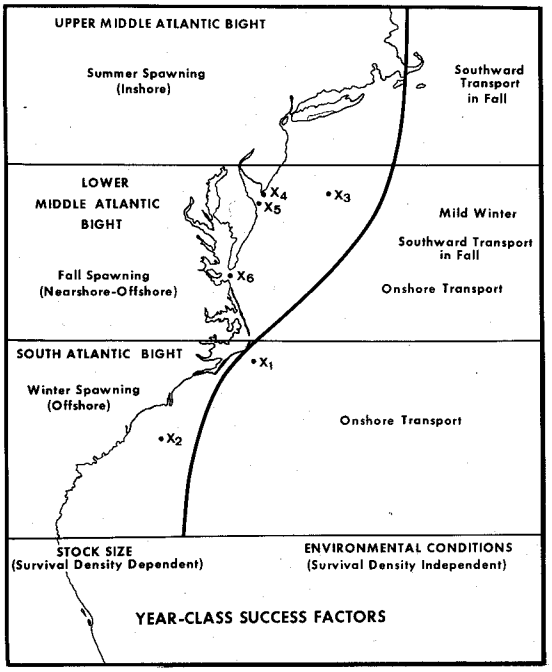

FIGURE 5.—Schematic representation of logic used in the development of the survival index predictive model. Location of environmental parameters used in the model is indicated by Xn, description of parameters in Table 4.

nificant spawning taking place farther offshore as adults migrate southward in the fall. This should result in increased significance of oceanic transport factors from north to south in the determination of year-class strength. The hypothesis of increasing importance of transport as spawning activities move progressively farther offshore is supported by the highly significant correlations between the survival index and transport values south of Cape Hatteras and similar correlations which have a lower level of significance off Delaware Bay.

The selection of locations and time periods for Ekman transport data was based on the availability of data for specific coordinates, desire for representation of broad spawning areas, and estimates of larval drift time and direction (Figure 5). Of the many possible environmental factors which could influence survival during the oceanic phase, three (transport, temperature, and river discharge) were chosen because they appeared to be factors of major importance and data series were available for the same period in which vital statistics of the Atlantic menhaden populations have been taken.

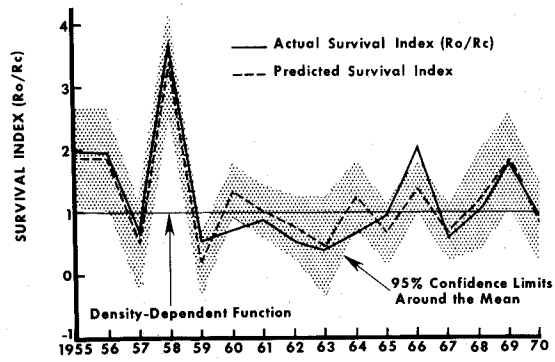

FIGURE 6.—Multiple regression of the survival index for Atlantic menhaden on environmental factors, 1955-70. Predictive equation and listing of environmental factors presented in text. Correlation coefficients and model data presented in Tables 4 and 6.

TABLE 6.—Data used in recruit-environment predictive model for Atlantic menhaden. Location of factors identified in Figure 5, individual factors identified in Table 4.

Year class	S.I.	Environmental factors X_1	X_2	X_3	X_4	X_5	X_6
1955	1.95	70	74	272	152	2.4	9
1956	1.94	64	107	307	271	1.0	30
1957	0.69	12	13	83	34	3.4	29
1958	3.64	94	124	141	169	0.6	9
1959	0.56	7	13	126	82	1.5	24
1960	0.71	40	42	121	78	1.6	11
1961	0.89	30	33	155	129	1.6	22
1962	0.54	27	63	149	79	1.4	17
1963	0.40	3	70	206	158	−0.3	9
1964	0.66	14	43	120	127	2.0	16
1965	0.96	11	32	96	35	1.8	7
1966	2.04	26	55	125	104	1.3	7
1967	0.61	4	21	98	63	1.8	8
1968	1.03	60	96	161	97	0.0	23
1969	1.82	92	76	317	212	0.4	16
1970	0.94	39	47	185	156	0.2	28

The multiple-regression model developed to relate recruitment to environmental variables yields a correlation coefficient of 0.919, significant at 0.003 with 9 df (Figure 6). Model data are given in Table 6. The model accounts for over 84% of the variance in the actual survival indices (Table 4). Translated into recruits, the model indicates that over 84% of the variation between actual recruitment into the fishery and expected recruitment during the 1955-70 period is accounted for by environmental fluctuation. The model is described by the equation:

$$S.I. = 0.4148 + 0.0205X_1 + 0.00530X_2 - 0.00807X_3 + 0.00950X_4 + 0.23967X_5 - 0.02679X_6 \pm e$$

where $S.I.$ = survival index computed by dividing observed recruits by expected recruits

X_1 = sum of monthly average zonal (westward) Ekman transport rates for January-March of the year-class year at lat. 35°N long. 75°W

X_2 = sum of monthly average zonal (westward) Ekman transport rates for January-March of the year-class year at lat. 33°N, long. 78°W

X_3 = sum of monthly average zonal (westward) Ekman transport rates for November-December of the year prior to the year class and January-February of the year-class year at lat. 39°N, long. 72°W

X_4 = sum of monthly average zonal (westward) Ekman transport rates for November-December of the year prior to the year class and January-February of the year-class year at lat. 39°N, long. 75°W

X_5 = minimum mean sea surface temperature at the mouth of Delaware Bay in the year-class year

X_6 = sum of monthly average discharge rates from Susquehanna, Potomac, and James rivers in July-September of the year preceding the year-class year

e = error term.

The predicted number of recruits for each year is given by:

$$R_p = R_{ci} \times S.I.$$

where R_p = predicted number of recruits

R_{ci} = number of recruits calculated from the Ricker curve at spawning stock size in the ith year.

A correlation between the observed number of recruits (R_o) and the predicted recruits (R_p) for each year yields a coefficient of 0.943 and a slope of 0.914 with no systematic bias around the regression line. Further evidence of the validity of the model is the failure of adjustments to increase the percent of variance accounted for by the environmental factors. The initial model, based on judgments of the proper time and location of environmental parameters, yielded a higher correlation coefficient than any subsequent models in which any of the parameters or time-spans were varied away from those which were considered the most significant from a biological standpoint. The parameters were not selected by a screening process from a large number of variables, but were selected because of their probable impact on survival.

The four largest year classes (1955, 1956, 1958, and 1969) during the 16-yr period are accurately described by the model. The average error of prediction for these years is 4.3% and the maximum error is 6.3%. Smaller year classes are not described with the same degree of accuracy, although the mean error for the 16-yr period is reduced from 1.5 billion fish using only the Ricker curve to 610 million individuals per year by the model, and the standard error of the mean is reduced from 501 to 155 million fish.

The multiple-regression model has a high correlation coefficient and therefore describes the data well. Its value for prediction is somewhat more tenuous and requires testing on a subsequent set of data to determine its accuracy. The model was not broken into separate time-series units for testing because of the brevity of the 16-yr data base.

The model is a first-cut approximation for the evaluation of transport and other factors. The number of variables included tends to increase the R^2 value, even though some parameters do not show individual significance levels when correlated with the survival index. However, only the Chesapeake Bay discharge has a β value of which ± 2 standard errors encompasses 0, indicating that the factor is probably not significant. The other parameters are associated with the same major air mass movements, and are therefore interrelated. A more sophisticated model should be based on either principal components regression or Ridge regression techniques to correct for the interdependence of some of the parameters and to improve the predictive capability. A reduction in the number of variables used is desirable from a statistical standpoint because of the short time span of the data base. Regression of the survival indices on the three transport values off of Cape Hatteras (lat. 35°N, long. 75°W) and Delaware Bay (lat. 39°N, long. 72°W; lat. 39°N, long. 75°W) yields an R^2 of 0.741 (12 df, $P<0.001$). The abbreviated model accounts for a significant portion of the variance around the spawner-recruit curve. It describes the data for high and low survival years nearly as well as the full model and probably has a similar predictive capability. Determination of the actual influence of the other factors (dis-

charge and temperature) which were included because of their potential biological importance will require a greater knowledge of spawning intensities and a longer term data base.

Overall, the model implies a predictive capability for large year classes and for extremely poor year classes. The model provides a satisfactory indication of the general magnitude of a year class prior to entering the fishery in 14 of the 16 yr.

For initial model purposes, the survival index was not computed beyond 1970 because the 1971 year class is still being harvested by the fishery, and the total catch from that year class necessary for verification of the number of recruits is not known. Forecasting in real time can be accomplished by inserting the routinely available environmental data into the survival index equation. The expected number of recruits for a given year class is obtained by determining age structure and abundance of 2-yr-old and older fish from fishery landings the previous fishing season, estimating an exploitation and survival rate to determine the number that will survive to spawn the next year class, calculating the expected number of eggs produced, and estimating the expected number of recruits from the Ricker function. Multiplying the expected number of recruits by the predicted survival index gives the predicted number of recruits. Estimates of the number of recruits can be made as early as April of the year-class year, and can be revised when actual exploitation rates are determined to allow better estimates of the size of the spawning stock which produces the year class. Thus, an initial prediction of the number of recruits can be made approximately 1 yr before they become available to the fishery the following spring.

DISCUSSION

Refinement of the predictive capability of the recruit-environment model is dependent on increased knowledge of the biology of Atlantic menhaden and on better understanding of the effects of the many factors that influence distribution, abundance, and survival. The model is concerned only with variation introduced into year-class size during the relatively short life phase in which larvae are oceanic and before metamorphosis takes place. The model concentrates on those factors which influence larval distribution and act as a mechanism to transport larvae into the vicinity of estuarine nursery grounds, thereby increasing survival. Major sources of variation such as food availability and predation have not been directly considered. However, since these factors are, to some extent, influenced by the number of larvae produced by the spawning stock, variations induced by them should be partially accounted for by the density-dependent Ricker function. The actual fluctuation in availability of food could only be determined by broad-scale surveys over the entire menhaden spawning range and would require a continuous time series for a number of years. Likewise, the determination of predation and cannibalistic influences would require extensive field surveys and controlled laboratory experiments.

Problems in determining the influence of pertinent environmental factors are compounded by the large geographic range of menhaden spawning activities. The influence of any one particular factor at a specific location could only be determined if the amount of spawning at that location was known. Comparison of environmental factors against a survival index for the entire stock, as has been done in this study, requires the selection of broad-scale factors having major influence over large portions of the spawning range, or the selection of representative data which provide a generalized environmental index for a selected factor. Localized variations may be highly significant, but masked by overall survival success or failure without knowledge of localized spawning intensity.

Cushing (1969, 1974) cited failures in attempts by other authors to correlate year-class strength and winds (or pressure gradients), and suggested that variation in wind direction may be a greater source of variation than the strength of winds from a single direction. The U.S. east coast is composed of an almost continuous series of bays and sounds, which extend both north and south of the major spawning region for Atlantic menhaden. Under these circumstances, variations in wind direction would probably influence the route of larval drift. However, unless northward or southward larval movement was extreme, larvae would not be transported away from suitable nursery areas as long as there was a significant onshore component of wind-driven circulation. Thus wind direction would be a significant factor only if that direction reduced the westward component of Ekman transport or if the normal seasonal wind pattern reversed, generating eastward (offshore) transport.

Comparison with Pacific Sardine

Computed survival indices allow comparisons between the Pacific sardine and Atlantic menhaden, in addition to those detailed by McHugh (1969). Radovich (1962) presented data for Pacific sardine showing the effect of good, average, and poor environmental conditions on the spawner-recruit relationship. He used maximum and minimum parabolas based on highest and lowest recruitment years and identified the area between the curves as indicative of the effects of the environment as well as spawning stock size on recruitment. A similar approach, modified by using the right-hand skewed Ricker curve yields similar results (Figure 7). Year classes used in the computation of the maximum and minimum recruitment curves for Atlantic menhaden were not selected for high and low recruitment as was done by Radovich, but were selected because they represented extremes in the variation of transport factors. The maximum recruitment curve was developed from year-class size during the 3 yr of highest (≥700 metric tons/s·km) southern onshore transport (1955, 1958, 1969). Similarly, the minimum recruitment curve was computed from year-class size during the 3 yr of lowest (<100 metric tons/s·km) onshore transport (1959, 1963, 1967). The two curves represent a wide range of environmentally induced fluctuation around the stock and recruitment curve calculated from the 1955-70 data base. No statistical significance can be attached to the upper and lower curves because each is based on three data points. However, the figure indicates the range of variance that masks the density-dependent function if pertinent environmental factors are not identified and weighted for effect at various stock sizes. The greater slope of the maximum curve is of particular interest, indicating a significant loss of potential recruits in good environmental years if adequate stock size is not maintained.

Additional parallels can be drawn between Pacific sardine and Atlantic menhaden spawner-recruit relationships during periods of overfishing and low survival. A comparison of spawning stock size and year-class size for the two species linked in chronological order shows striking similarities (Figure 8). In each case, there was a period of several years at high stock size in which the size appeared to be near or past the maximum needed to produce large numbers of recruits. A series of

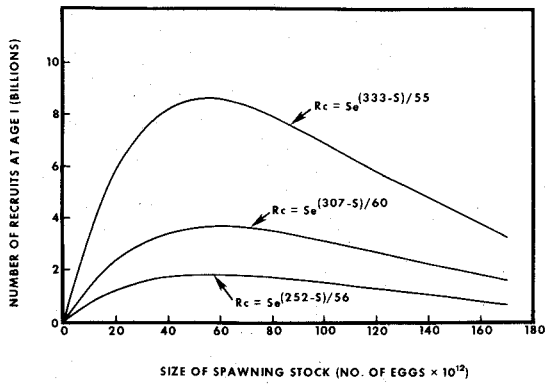

FIGURE 7.—Ricker spawner-recruit relationships calculated for years of good and poor environmental conditions. The upper curve is calculated from observed recruitment during the three greater years of Ekman transport, the middle curve is calculated from the 16-yr data set, and the lower curve is calculated from observed recruitment during the three lesser years of Ekman transport.

good year classes (1937-39 for sardine; 1955, 1956, and 1958 for menhaden) was followed by a series of poor survival years (1940-45 for sardine, 1959-64 for menhaden). These reductions in recruitment, combined with excessive fishing pressure, reduced spawning stock size drastically, leading to a restabilization of stock and recruitment around small stock levels. In the case of menhaden, the 5-yr period of decline reduced the spawning stock size by an order of magnitude. By 1966, spawning potential had dropped to a low of 5×10^{12} eggs from the 1961 high of 165×10^{12}. The parallel between the two sets of data is a cause for concern, because the decline and apparent restabilization of Pacific sardine stocks was followed by a complete collapse of the fishery. Henry (1971:23) in his analysis of the decline of the Atlantic menhaden fishery stated, "I am concerned that the stocks of Atlantic menhaden may have been reduced to a level that is having an adverse effect on recruitment." Clark (1974:14), in a study of the effects of schooling on population dynamics on small schooling species (as in the case with Atlantic menhaden), concluded that, "A commercial fishery based on such a species might be expected to experience a rather spectacular population collapse, which could be brought on either as a direct result of an increased fishing effort which suddenly transforms the system into an unstable mode, or as an indirect result of fishing which reduces resiliency and renders the population vulnerable to the effects of random environmental fluctuations." The possibility of a complete collapse in the Atlantic

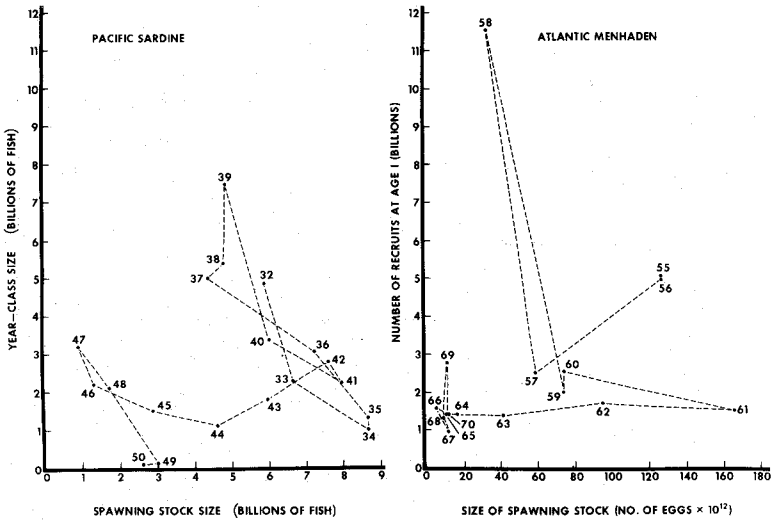

FIGURE 8.—Year-class size related to spawning stock size and linked in chronological order for Atlantic menhaden and Pacific sardine. Pacific sardine figure after Radovich (1962:134).

menhaden fishery, given high fishing effort and additional years of poor survival, cannot be discounted.

Fortunately, there are significant differences in the environment, biology, and fishery of Pacific sardine and Atlantic menhaden. One of the more important differences is the estuarine dependence of menhaden. In every year, at least some estuarine systems on the east coast should provide favorable environments, insuring good survival of larvae which reach those nursery grounds. Also, spawning activities spread over the entire coast should include at least some areas conducive to survival, reducing the chance of almost no survival over the entire range. Climatic change which shifts the distribution of menhaden spawning activities would not likely shift the spawning region far enough away from suitable nursery areas to cause the type of massive failure that occurred in the sardine fishery. Another significant factor in the collapse of the sardine stocks was an increase in the stock size of competing species, filling the niche in the ecosystem as the sardine population decreased. Although there is no fishery for species which are potentially competitive with Atlantic menhaden and adequate stock data on such species are not available, there are no indications of large increases in abundance of any coastal pelagic species, and the niche available to menhaden appears to be open. However, John Radovich (pers. commun., California Department of Fish and Game) points out that "the value of not having identified an increase in competitors for the menhaden may be of little significance because:

1) The sardine collapse and failure to recover may have happened without a 'competing' species such as the anchovy.
2) Available forage and habitat may be utilized through slight increases in the abundance of several species, and hence go unnoticed.
3) The capacity within a trophic level may vary considerably so that actual changes in the abundance of competing species may be masked by changes in available forage and habitat."

The menhaden fishery is somewhat self-regulating, in that low stock levels have brought about economic conditions which forced a reduction in effort and closure of processing plants. The closure of plants in the northeast United States during the late 1960's reduced fishing effort on older age-groups, halting the drastic decline in spawning stock size (Schaaf in press). This action, plus good survival in 1966 which produced the spawning stock for the high transport, large year-class year of 1969, is probably responsible for the brief resurgence of the fishery in the early 1970's.

Implications for the Fishery

Implications for the fishery are rather straightforward: in years of poor environmental conditions recruitment is low regardless of stock size; extremely low spawning stock sizes in years of poor environmental conditions result in recruitment below the level needed to maintain the fishery; favorable environmental years will

produce exceptional year classes and a proportionally greater harvestable surplus at stock sizes near the spawning optimum; and a series of poor environmental years (1959-64), coupled with excessive fishing pressure, will reduce stock size to a level which produces little harvestable surplus.

During the 16 yr covered by this study extremely large year classes were produced in 3 yr (1955, 1956, and 1958). Favorable conditions in 1969 resulted in a high survival rate, but only produced 2.7 billion recruits because of small spawning stock size. In one other year (1966) survival occurred that was greater than expected, but at extremely low stock size. In the other 11 yr recruitment was either near, or well below the expected level, compounding the stock depletion caused by excessive fishing pressure. The drastic reduction in stock size resulted in a restabilization of the stock-recruitment relationship around a low stock level. This is evidenced by the steady decline in catches from 1956 to a low of 162,000 metric tons in 1969, followed by slightly higher catches in succeeding years (Table 7). Extremely large catches in the late 1950's are the result of the unusual coincidence of 3 high survival years within a 4-yr span. Average survival over the 16-yr period was much lower, and average year-class size would be considerably smaller, even at optimum spawning stock size.

Schaaf and Huntsman (1972) gave MSY estimates for Atlantic menhaden of 600,000 metric tons based on an equilibrium catch-effort curve from historic data and 380,000 metric tons from a population-prediction model. The population-prediction model dampens the effects of large year classes and probably comes closer to representing long-term MSY than the higher estimates.

The maintenance of optimum spawning stock size and several year classes in the spawning stock is vital to insure adequate response to favorable environmental conditions. Based on the estimated survival rates over the 16-yr period, and the optimum spawning stock size from the Ricker function, surplus yield was calculated under conditions which would maintain four spawning groups (ages 3-6) in the populations. The calculation of surplus yield is based on an instantaneous natural mortality of 0.42 and fishing mortality of 0.36 spread over 6 yr within a year class (ages 1-6) and assuming that one-half of the age-1 recruits are vulnerable to the fishery. A full complement of years 1-6, from year-class data available after 1954, was not obtainable until 1961, when 6-yr-old fish were harvested from the 1955 year class. Under the conditions imposed on the harvest, the allowable catch, computed for 1961-71, averaged 419,000 metric tons/yr (Table 7). Extremes in the allowable catch would have ranged fron 227,000 to 633,000 metric tons, depending on the size of year classes which constituted stock size in a particular year. This catch is similar to the MSY estimates of Schaaf and Huntsman (1972), and was computed for a period in which most of the year classes had less-than-expected survival. The survival index was well below 1.0 from 1959 to 1964, a period of six continuous years, and is reflected by the decline in surplus stock during that period. Actual catches made by the fishery from 1955 to 1971 (Table 7) averaged approximately the same as MSY, but

TABLE 7.—Catch of Atlantic menhaden at MSY for actual survival rates, 1955-70 year classes, fishery landings, 1955-71, and predicted surplus from recruit-environment model.

	Potential catch at *Sm*			Actual catch by fishery			Predicted catch
Year of harvest	No.in billions	Wt (thousand metric tons)	Wt/fish (g)	No.in billions	Wt (thousand metric tons)	Wt/fish (g)	Wt (thousand metric tons)
1955				3.12	641.4	206	
1956				3.56	721.1	203	
1957				3.51	602.8	172	
1958				2.72	510.0	188	
1959				5.35	659.1	123	
1960				2.78	529.8	191	
1961	1.68	632.9	377	2.60	575.9	222	510.9
1962	1.38	488.1	354	2.01	537.7	268	466.7
1963	1.10	410.0	373	1.76	346.9	197	412.5
1964	0.88	339.0	385	1.73	269.2	156	392.5
1965	0.76	226.6	298	1.50	273.4	182	295.5
1966	0.99	254.9	257	1.34	219.6	164	374.2
1967	1.72	367.4	214	0.98	193.5	197	371.5
1968	1.62	472.0	291	1.14	234.8	206	405.1
1969	1.40	426.0	304	0.87	161.6	185	387.0
1970	1.81	464.7	257	1.40	259.3	185	471.5
1971	1.78	525.6	295	0.97	250.3	258	521.6
Mean	1.37	418.8	306	2.20	410.4	178	419.0

were taken by extensive overfishing in the late 1950's and early 1960's, with a resultant decrease in spawning stock size and age structure. The average catch from 1955 to 1963 was 596,000 metric tons, well above the MSY level. The fishery also took greater numbers of fish of smaller size than was compatible with management to insure adequate numbers of spawners. Thus overfishing, which reduced stock size, was compounded by a series of poor environmental years, further reducing the spawning stock to a level below that necessary to provide large surplus yields from the higher survival years of 1966 and 1969. Had optimum spawning stock size been maintained, the fishery should have been able to increase its yield during the 1967-71 fishing seasons by an average of 231,000 metric tons/yr.

The value of a predictive model lies in its usefulness for developing strategies to take advantage of exceptional year classes or to avoid overexploitation of poor year classes. Catches based on the number of recruits calculated from the survival index model are similar to MSY and to those averaged by the fishery (Table 7). However, the absolute mean error from the allowable surplus is approximately 134,000 metric tons/yr for the actual fishery landings (1961-71) and 48,000 metric tons/yr if harvest had been limited to the predicted surplus. Some overfishing would have occurred because of errors in prediction, but it would have been significantly less than that imposed by the fishery during earlier years. Fishing at a level necessary to harvest the predicted surplus would have provided reasonably stable catches, maintained several age-classes in the fishery, maintained adequate spawning stock, and prevented excessive exploitation of the stocks, all desirable factors in the management of fishery resources.

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