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Steven M. Atran
Virginia Institute of Marine Science

Joseph G. Loesch
Virginia Institute of Marine Science

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Steven M. Atran[**]
Joseph G. Loesch

School of Marine Science, Virginia Institute of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

Analyses of time series of commercial catch statistics are usually made with an implied assumption that catchability remains constant. Although the annual catchability from year to year may remain fairly constant, this assumption is rarely, if ever, valid for catchability within a season. Changes in catchability, abundance, and fishing all contribute to fluctuations in the catch from a fish stock (Clark and Marr, 1956; Pope and Garrod, 1975). Behavioral changes due to size or age may cause variations in catchability (Morrissy and Caputi, 1981). By examining the within-season changes in catchability, it may be possible to discern properties of a stock that are not apparent when only annual time intervals are examined.

The objective of this study was to develop a means to estimate weekly within-season catchability coefficients of a stock and to demonstrate how examination of these short-term fluctuations might be useful in a stock analysis. Atlantic menhaden, *Brevoortia tyrannus,* was selected as a model because of the availability of a time series of weekly catch-at-age data for this species.

Methods

Data

Weekly menhaden catch-at-age (in numbers) and vessel-landings data from 1968 to 1982 were made available by the Beaufort Laboratory, National Marine Fisheries Service (NMFS), Beaufort, North Carolina. Migrating menhaden stratify by age and size (Nicholson, 1971b); therefore, the stock was divided into age groups to eliminate differences in catchability due to age-specific (and size-specific) migration patterns.

Calculation of weekly abundances

Abundance estimates with constant time intervals of one week were needed to allow between-year comparisons of weekly catchability and to conform to the Beaufort Laboratory's system of reporting catches. Such short time intervals usually resulted in consecutive intervals of zero catches commonly occurring near the beginning and end of a sequence of weekly landings data for a given year and age group.

Murphy (1965) developed a method for estimating abundance and fishing mortality rates on a cohort of fish when catches are known within time intervals and when an estimate of instantaneous fishing mortality for one time interval and natural mortality for all time intervals are available. A restriction on this method is that the time intervals must be of equal duration and that each time interval must contain catches. Tomlinson (1970) presented a generalization of Murphy's method, which allowed for variable time intervals and zero catches, provided that the first and last time intervals each contain catches and that two or more consecutive zeros do not occur.

The normal method for ensuring that consecutive zero's do not occur in the catch data is to pool time intervals containing zero catches with adjacent nonzero intervals. In this study it was desirable to keep the time intervals fixed, even if it results in consecutive zeros in the catch data. A modification of Tomlinson's method was used, which allows for any number of consecutive zeros, provided that the first and last time intervals contain catches.

Extension to Tomlinson's model

A catch ratio, R_i, can be constructed between catch in the current and subsequent time interval. The ratio for interval i is given by (Eq. 4 in Tomlinson, 1970)

$$R_i = \frac{C_{i+1}}{C_i} = \frac{e^{-t_i(F_i+M_i)}E_{i+1}}{E_i}, \quad (1)$$

where C_i, C_{i+1} = number of fish caught in time intervals i, $i+1$;

F_i = instantaneous fishing mortality in time interval i;

M_i = instantaneous natural mortality in time interval i;

E_i, E_{i+1} = exploitation rate in time intervals i, $i+1$.

If catch in time interval $i+1$ is zero, then the ratio R_i is zero and the subsequent ratio R_{i+1} is undefined. In this case, the ratio can be constructed between the current time interval and the second subsequent interval. This ratio (R_{i+1}) is given by Equation 5 in Tomlinson, 1970, as

$$R_{i+1} = \frac{C_{i+2}}{C_i} = \frac{e^{(-t_i(F_i+M_i)-t_{i+1}M_{i+1})}E_{i+2}}{E_i}. \quad (2)$$

The above equation is Tomlinson's extension to Murphy's catch equation. This can be further extended to include any number of intermediate time intervals with zero catch. A generalized form of the catch ratio between any two time intervals i and $i+k$, where the catches for all intermediate time intervals is zero, is

$$\frac{C_{i+k}}{C_i} = \frac{E_{i+k}e^{-t_i(F_i+M_i)-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{E_i}. \quad (3)$$

Given an estimate of natural mortality rate and fishing mortality rate for the final time interval, F_i's for the previous time intervals can be solved by estimating $E_i \times \exp[t_i(F_i+M_i)]$. This can be estimated from E_{i+k} by rearranging Equation 3 as

$$E_i e^{t_i(F_i+M_i)} = \frac{C_i E_{i+k}e^{-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{C_{i+k}}, \quad (4)$$

where C_i is nonzero, and all catches between t_i and t_{i+k} are zero. F_i may be found by iteration after inserting the result of Equation 4 in the following equation (Equation 9 in Tomlinson, 1970)

$$E_i e^{t_i(F_i+M_i)} = \frac{F_i(e^{t_i(F_i+M_i)} - 1)}{F_i + M_i}. \quad (5)$$

Once the F_i's have been estimated, the E_i's can be estimated by inserting the value of the above equation into the following:

$$E_i = \frac{(\text{the value of Equation 5})}{e^{t_i(F_i+M_i)}}. \quad (6)$$

After calculating the E_i's and F_i's, the population size at the start of each time interval (N_i) can be estimated from

$$N_i = \frac{C_i}{E_i}, \text{ where } E_i <> 0. \quad (7)$$

To demonstrate the use of this extension to Tomlinson's method for solving the catch equation, the computer program MURPHY (Abramson, 1971), which implements Tomlinson's model, was modified to incorporate the extension for consecutive zeros to estimate weekly abundance and fishing mortalities for the Atlantic menhaden purse-seine fishery. The catch data were broken up into weeks and into age groups within a week.

Constant parameters used

In addition to catch-at-age data, virtual population analysis (VPA) requires estimates of instantaneous natural mortality for all time intervals and an estimate of instantaneous fishing mortality for one time interval. Natural mortality was assumed constant and a weekly value of 0.0087 (annual M=0.45) was adopted on the recommendation of the Beaufort Laboratory. Estimates of fishing mortality for the final week of landings data in each year were obtained from Table 13 of Broadhead et al.[1] for the years 1968–76 and for age groups 0–5. For age groups 6–8 the values for age 5 were used. For the years 1977–82, the average values for the years 1968–76 for each age group were used (1968–75 for age group 0). In each case, the annual value of F from the table was divided by the number of weeks in the year that had landings data to obtain a weekly F. Instantaneous fishing mortality values were probably overestimated because catch generally declined at the end of the season. However, in the backward solution to the catch equation, the value for F tends to converge toward its true value for a given M. Therefore, the error in abundance estimates due to this overestimation of F should be minor at the beginning of each year's landing data, although it may result in the underestimation of abundance toward the end.

Defining effort

An index of fishing effort was needed to calculate a catchability coefficient. The number of vessels with landings in a given week (vessel-week) is commonly used as the unit of fishing effort in studies of the menhaden purse-seine fishery and was the unit used in this study. Menhaden vessels generally operate continuously throughout all or part of the fishing season, fishing every day, as weather permits, un-

[1] Broadhead, G., C. Grimes, J. Loesch, W. Nelson, G. Sakagawa, and K. West. 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. manuscr., 68 p.

less they are in port for repairs. Any time period that assumes continuous fishing and accounts for unproductive fishing days should be a satisfactory unit of fishing effort (Nicholson, 1971a). Number of landings as a unit of effort assumes continuous fishing. Although the number of days that a given vessel was fishing in a week was unknown it was assumed that variations were randomly and normally distributed.

Calculation of weekly catchability coefficients

The catchability coefficient is defined as the fraction of a fish stock that is caught by a defined unit of fishing effort (Ricker, 1975). The relation between catch, effort, abundance, and catchability is

$$\left(\frac{C}{f}\right)_t = q_t N_t, \qquad (8)$$

where $(C/f)_t$ = average catch per unit of effort over period t; N_t = average abundance during period t; and q_t = catchability during period t.

The VPA estimates of abundance are for the beginning of a time period. For the short, one-week time periods used in this study, average abundance in a period is assumed to approximate $(N_t + N_{t+1})/2$. Average catch per unit of effort in a time period can be calculated as total catch divided by total effort for that period. The above equation can thus be rearranged to define the catchability coefficient as

$$q_t = \frac{\left(\frac{C_t}{f_t}\right)}{\left(\frac{N_t+N_{t+1}}{2}\right)}. \qquad (9)$$

This equation was used to calculate initial weekly catchability coefficients for each age group. No catchability estimate was made for weeks in which there was no catch landed for the age group considered. Also, no catchability estimate was made if abundance estimates were not made for both the week being considered and the following week, because the average abundance during the week $(N_t+N_{t+1}/2)$ was used to estimate catchability.

Statistical analysis

Weekly abundance estimates at age were made in each year from the first week in which a catch was landed until the last. Catchability coefficients by age were estimated for each week for which there were abundance estimates for the current and subsequent weeks. Friedman's method for randomized blocks
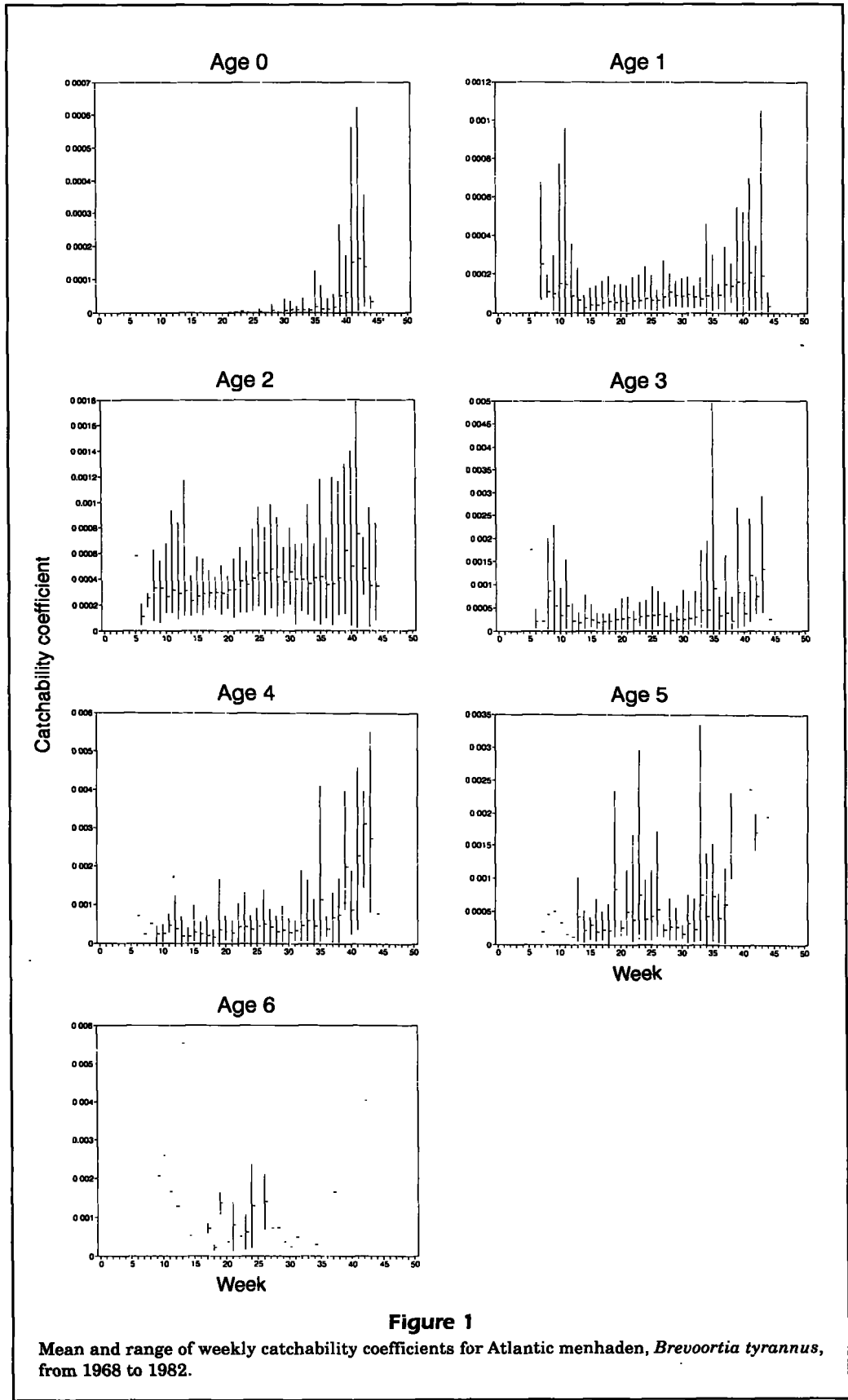
(Sokal and Rohlf, 1981) was used to test for significant differences in annual patterns of weekly catchability coefficients for each age group between years. This is the nonparametric analog to the parametric analysis of variance (ANOVA) randomized complete block design, but the rankings of the variates within each block are used rather than the actual measurements. A nonparametric test was used because the relative degree of weekly fluctuations from year to year may vary owing to biotic or abiotic factors. Thus, heterogeneity of variance between years may be expected, making a parametric model inappropriate.

Results

The Friedman's test indicated that at least one year was significantly different from the others at the 0.05 alpha level for age groups 1, 2, 3, and 4 but not significant for the remaining age groups. Subsequent multiple comparisons for these age groups with Friedman's rank sums (Hollander and Wolfe, 1973) failed to show temporal differences. These differences were therefore considered to be random variations about a mean, allowing the annual variations for each week to be averaged to determine the underlying pattern.

Plots of high, low, and mean weekly catchability were created for each age group (Fig. 1). For most age groups the range of catchability coefficients was greater at the beginning and end of the season than in the middle. The plots were examined visually for signs of fluctuation within a season. The graphs of weekly catchability showed the following pattern: the first part of the catchability curve features an initial peak followed by a rapid decline. This decline is followed by a gradual increase in catchability as the season progresses, then by a second sharp peak near the end of the season. The height of the initial peak relative to the rest of the plot is most pronounced in age-1 and age-2 fish. It becomes less pronounced and disappears altogether as the fish become older. This first peak does not occur for age-0 menhaden, which are subject to a fishery that is largely directed against catching them in the fall.

The catchability graph of age-0 menhaden differs from the other age groups. This age group is not targeted during most of the year but becomes subjected to a directed fishery off North Carolina in the fall. Catchability for this age group remains at or near zero for most of the season because no age-0 fish are being caught. Near the end of the season, it rapidly rises from zero to a peak and then quickly drops back to zero as the fishery ends.

Figure 1

Mean and range of weekly catchability coefficients for Atlantic menhaden, *Brevoortia tyrannus*, from 1968 to 1982.

Discussion

Virtual population analysis assumes that there is complete recruitment for a set of age classes and that availability remains constant for all recruited age classes. The existence of sharp initial and ending seasonal catchability peaks is probably due to underestimation of abundance at the beginning and end of the season from the VPA method. This indicates that VPA can be biased when availability fluctuates. Virtual population analysis measures the "virtual" abundance, that which appears to the fishery to be there, rather than absolute abundance. Early in the season, when the menhaden are migrating into the fishing area from their wintering grounds, only part of the stock is available for exploitation. Changes in availability, or accessibility, can affect the catchability coefficient (Cushing, 1968). Marr (1951) showed that catchability is directly related to availability. However, because VPA assumes that there is full availability, abundance is underestimated. If the abundance is underestimated, then the catchability coefficient will be overestimated (Shardlow and Hilborn, 1985).

Theoretically, this first peak should extend to infinity prior to the start of the season when VPA is used to estimate abundance, because availability at this point in time is zero. If abundance had been measured with a method independent of the fishery catch statistics, such as mark-recapture, catchability estimates would have been based on absolute rather than on virtual abundance and there would not have been an early season peak. The rise from zero or near-zero catchability which occurs in many of the plots, particularly with older age groups, may be due to an earlier or faster migration of these age groups into the fishing area or to more complete recruitment of the age group at the start of the season. Younger age groups are not completely recruited into the fishery, but by age 2, the menhaden are fully recruited into the Atlantic coast purse-seine fishery (Atlantic Menhaden Management Board, 1981). If availability is at or near maximum by the time of the first catch, VPA will not underestimate abundance, and consequently catchability will not be overestimated. One advantage of examining within-season fluctuations of catchability, therefore, may be to assess when the stock becomes available to the fishery.

After the initial peak, a gradual rise in catchability can be seen as the season progresses, most likely due to a decrease in abundance during a period of full availability. This observation is consistent with Schaaf (1975), who reported a logarithmic inverse relation between annual values of catchability and abundance of menhaden. An increase in this rate might result if stock abundance during the season were decreasing faster than normal, and it would then be an indicator of overfishing.

The pattern of catchability for age-0 menhaden differs from that of the other age groups in that there is no initial peak and landings begin much later in the season (Fig. 1). Age-0 menhaden are fished extensively in the North Carolina fall fishery which is largely directed toward these fish. Paloheimo and Dickie (1964) stated that when fishermen selectively apply their effort toward some schools, the result is variance in the catchability coefficient depending on age, species, and relative abundance. This effect is apparent in the plot of average weekly catchability coefficient for age-0 menhaden. When the age-0 menhaden, commonly referred to as "peanuts," migrate out of Virginia and North Carolina estuaries, they become readily available close to shore where they dominate the landings, usually in December and January.

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