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FLUCTUATIONS IN THE CATCHABILITY COEFFICIENT OF ATLANTIC MENHADEN, 1968-1982

A Thesis

Presented to

The Faculty of the School of Marine Science The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

Steven M. Atran



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APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirements for the degree of

Master of Arts

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Approved, August 1986

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FLUCTUATIONS IN THE CATCHABILITY COEFFICIENT OF ATLANTIC MENHADEN, 1968-1982

ABSTRACT

Weekly estimates of Atlantic menhaden abundance were derived from catch at age data for the years 1968-1982. Initial estimates of weekly catchability coefficients were calculated from the estimates of abundance and catch and effort data. Plots of the average weekly catchability coefficients for age groups 0 to 5 revealed patterns of fluctuations within a season. Between year fluctuations in catchability coefficients were found to be significantly different after accounting for the within season variation. Age groups were tested separately to eliminate age dependent variation as a possible cause of fluctuation. The relationship between catchability and abundance was calculated: predicted values of the catchability coefficient based on abundance were subtracted from the original estimates. Significant differences were also found between years for these residual catchability coefficients, thus factors in addition to abundance must contribute to between year variation in the catchability coefficients. Potential factors affecting catchability coefficients. Potential factors affecting catchability coefficients are cyclic changes, long term trends, density-dependent changes, density-independent changes, and changes due to changes in fishing effort.

FLUCTUATIONS IN THE CATCHABILITY COEFFICIENT OF ATLANTIC MENHADEN, 1968-1982

INTRODUCTION

Atlantic Menhaden - Historical Perspective

In 1621, the Indian, Squanto, showed English settlers at Plymouth, Massachusetts how to fertilize their crops with fish. Among the fish used was one the Indians called Munnawhatteaug, which means fertilizer (Frye 1978). It is from this that the name menhaden is derived. There is evidence that Squanto actually learned this method from other Europeans only a few years earlier, while he was in Europe as a slave (Ceci 1975).

The commercial fishery for menhaden began in Rhode Island in 1811. At that time, menhaden were boiled to extract the oil. Later, more efficient ways of extracting the oil were developed, and fish meal and solubles became commercially important. By the 1850's, menhaden processing plants had been established in Massachusetts and Connecticut, and in Maine by 1864. The solid material left after the oil was extracted was made into guano and sold for fertilizer (Frye 1978).

Floating factories were built in the 1870's to follow the movements of the menhaden schools and reduce the time required for the catch to reach the factory. By the late 1870's, however, floating factories were going out of use because of the introduction of steamers to the menhaden

fishery (Frye 1978).

During the Civil War, Union soldiers stationed in the south noticed the abundance of menhaden in inshore waters. As a result of their observations, the menhaden fishery, which had previously existed only in the north, spread southward. By 1889 processing plants existed as far south as North Carolina (Hart 1983).

Menhaden were initially caught with haul seines or gill In 1826, the purse seine was invented by John Tallman nets. and Christopher Barker, who had started the first menhaden processing plant in Rhode Island in 1811 (Frye 1978). Purse seines came into general use during the next 40 or 50 years. Sailing vessels were used initially to operate the purse Coal-fired steamers came into use after the Civil seines. War, and these were replaced by diesel powered vessels in the 1930's (Hart 1983). The use of spotter planes began in the 1940's to guide menhaden boats to the schools (Frye 1978). More recently, technological advances such as nylon nets, pumping of fish from the nets to the hold, hydraulic winches and power blocks have allowed the menhaden fishery to operate more and more efficiently.

Initially, menhaden were important for their oil, used in tanning and curing leather, paints, rope and soap making, and for fertilizer. They were also used for food in the 1700's. Today the primary use of menhaden is for poultry feed and pet food. A new use for menhaden meal is the manufacture of surimi, artificial crab meat. The oil is

used in various products including paints, soaps, lubricants, and lipstick. In Europe and in Canada the oil is used in the production of margarine (Henry et al. 1965, Frye 1978, Hart 1983).

In the 1950's and 1960's Atlantic menhaden was the largest commercial fishery in the U.S., peaking in 1956 at 712,000 metric tons (MT), worth about \$20 million (Henry et al. 1965, Davis 1983). Late in the 1960's landings underwent a drastic decline, bottoming out at 161,000 MT in 1969. Since then, landings have again increased to the 300,000 MT range, and reached 382,000 MT in 1982. Although the number of Atlantic menhaden now landed is as high as it was in the 1950's, the biomass landed is reduced, partly because of a heavy fall (peanut) fishery on young of the year menhaden. Atlantic menhaden landings, combined with landings from the Gulf menhaden fishery, continues to be one of the country's most important fisheries (Davis 1983).

Life History

Adults

The Atlantic menhaden stock is believed to constitute a single population (Nicholson 1971b, 1978). From January to March, menhaden of all sizes concentrate in the offshore waters from Cape Hatteras, North Carolina to northern Florida (Nicholson 1971b). The menhaden begin migrating inshore and northward In late winter and spring. They stratify by age and size at this time, with the older and

larger fish leaving first and migrating farther north (Nicholson 1971b). Maximum migration speeds of 11 to 16 km/day are reached (Dryfoos et al. 1973), and by June, the population is stratified by age and size along a north-south axis (Nicholson 1971b). Menhaden travel in surface schools, usually inside the 20 meter depth contour, although a few schools have been spotted as far out as the 55 m contour (Reintjes 1982).

In late summer, the menhaden north of Cape Cod, primarily age 4 and older, begin migrating southward (Nicholson 1971b). The southward migration begins in September off the coast of New Jersey, and by late November there are few menhaden left in the New York bight (Reintjes 1982). Along with menhaden from the Chesapeake Bay, the fish continue to move southward, eventually reaching their wintering grounds from Cape Hatteras to northern Florida during October to December (Nicholson 1971b).

Atlantic menhaden mature and begin spawning between ages 1 and 3, with most females maturing at age 2 (Higham and Nicholson 1964). In Virginia waters, menhaden are mature at about 1.5 years of age (McHugh et al. 1959).

Although menhaden spawn throughout the year, the time of spawning varies with location. In the north Atlantic, as far north as Nantucket Shoals, spawning apparently occurs from May to September. In the mid-Atlantic, there appear to be two spawning seasons, March through May and again in September and October. In the south Atlantic, spawning appears to be from October through March (Higham and Nicholson 1964). Menhaden in Virginia waters appear to have two spawning peaks, early winter and early spring (McHugh et al. 1959).

Spawning occurs in the open ocean in the mid-Atlantic and south Atlantic regions. In Virginia, spawning apparently does not occur in Chesapeake Bay, but does occur in the ocean not far outside the Virginia capes (Higham and Nicholson 1964, McHugh et al. 1959). Further north, however, eggs and larvae have been collected in harbors (Hildebrand 1963, Kuntz and Radcliffe 1917), suggesting that spawning occurs in harbors, although their presence may be due to transport.

Reported spawning temperatures for menhaden range from 9° C to 24.4°C (Herman 1963, Marak and Colton 1961, Marak et al. 1962), and salinity has been reported at 32.14 $^{\circ}$ /oo in a single observation by Marak et al. (1962).

Fecundity has been found to range from a mean of 38,000 to 631,000, with older fish producing larger numbers of ova (Higham and Nicholson 1964, Dietrich 1979). The eggs are highly transparent, buoyant and spherical, with a diameter of 1.4 - 1.6 mm. They contain a small oil globule, and are covered with a thin horny membrane (Hildebrand 1963).

Juveniles

Larval menhaden are more abundant in the upper 15 m of the water column than in the underlying waters, and wind driven currents (Ekman transport) appear to play a major role in their inshore movement to estuaries after $1 \frac{1}{2}$ to 2 months in the ocean (Nelson et al. 1977).

The larvae are 18 - 34 mm in length when they enter the estuaries (Nelson et al. 1977, Reintjes and Pacheco 1966). Entry occurs from May to October in the New England states, October to June in the Middle Atlantic states, and December to May in the South Atlantic states. The larvae at entry are slender, transparent, and nearly colorless except for several rows of melanophores. In the estuaries, they undergo metamorphosis into juveniles with deep bodies, well developed fins, ventral scutes, scales, and a large head. Their feeding habits change from selective predation upon individual particles to nonselective filter-feeding. The juvenile menhaden are polyhaline, tolerating salinities from less than 1 $^{\rm O}/{\rm oo}$ to hypersaline environments of 60 $^{\rm O}/{\rm oo}.$ They are found in water temperatures of 0° C to 40° C, but may suffer large mortalities if the water temperature drops below 3° C for several days (Reintjes and Pacheco 1966).

Menhaden school from the time they enter the estuary as larvae (Reintjes and Pacheco 1966). They leave the estuaries in the autumn and migrate south as far as Florida. In the spring, the age I juveniles redistribute northward, with the largest fish going furthest north (Kroger and Guthrie 1973).

Statement of Problem

Management of commercial fish stocks by control of

catch and/or effort is often based on models which assume that catchability, the fraction of a fish stock caught by one unit of fishing effort (Ricker 1975), remains constant throughout the fishing season. This assumption, however, is rarely, if ever, valid, and can cause analytical errors that can result in poor management.

There are many possible causes of variation in catchability. Behavioral change due to size or age may lead to variations in catchability, and has been reported to be one cause of variation for marron, Cherax tenuimanus (Morrissy and Caputi 1981). Density-dependence, or changes due to changes in abundance, has been demonstrated in some fish stocks, such as Pacific sardine, Sardinops sagax (MacCall 1975), Atlantic menhaden, Brevoortia tyrannus (Schaaf 1975), North Atlantic cod, Gadus morhua (Pope and Garrod 1975, Garrod 1977), capelin, Mallotus villosus (Ulltang 1976), and chinook salmon, Oncorynchus tshawytscha (Peterman and Steer 1981). See Appendix A for a complete discussion of types of fluctuation in catchability. Fluctuations in catchability, abundance, and fishing all contribute to fluctuations in the catch from a fish stock (Clark and Marr 1956, Pope and Garrod 1975).

If the fluctuation in catchability can be reduced by removing known causes of fluctuation, then management models in which catchability plays a role should give more accurate results. Furthermore, the remaining fluctuation may provide some insight into the behavior or availability of the fish stock, leading to further studies into the causes of fluctuation in catchability.

An inverse relationship between abundance and catchability of Atlantic menhaden (Brevoortia tyrannus) has been demonstrated by Schaaf (1975). Nicholson (1971b) showed that migrating menhaden stratify by age and size. Different migration patterns by fish of different ages results in different levels of accessibility to the fishery. Accessibility is a measurable modification of the catchability coefficient (Cushing 1968). Since the behavior of menhaden varies with age, this suggests that catchability also varies with age. If these are the only factors causing fluctuation in catchability, then removing the effect of age and abundance should leave a residual catchability coefficient which is constant except for random error or a possible cyclic variation, where the cycle occurs within the year. If there is still fluctuation, then there are other causes contributing to catchability, which can be clumped under the general term of availability.

Objectives

The first objective of this study was to determine whether the catchability of purse-seine caught Atlantic menhaden varies within a season, and if so, to qualitatively explain why such fluctuation exists.

A second objective was to determine whether such fluctuation follows a consistent pattern from year to year,

after removing known or suspected causes of fluctuation, specifically, age and density-dependence.

Hypothesis

When the effects of age and density-dependent variation in catchability are removed from the catchability coefficient, then the remaining residual catchability coefficient is constant or follows a consistent temporal pattern, and the following hypothesis is true:

 $H_0: q_t = f(t)$ with the alternative: $H_a: q_t \neq f(t)$

where: t = week of year
qt = catchability coefficient in week t
f(t) = an (unknown) function of time

The null hypothesis states that the value of q_t follows some unknown function of time. The alternative hypothesis states that q_t does not follow a function based on time.

If a constant catchability or consistent pattern exists, then the way in which catchability varies between weeks will not change significantly from year to year, and the hypothesis can be tested by comparing differences between years after removing the effect of variation between weeks. No assumption of normality or homogeneity of variance was made, and a non-parametric test, Friedman's method for randomized blocks (Sokal and Rohlf 1981), was used.

If the test showed differences between years, then

where those differences exist was shown by a non-parametric multiple comparisons test based on Friedman's rank sums (Hollander and Wolfe 1973).

MATERIALS AND METHODS

Data

Weekly menhaden catch-at-age and vessel landings data from 1968 to 1982 were made available by the Beaufort Laboratory, National Marine Fisheries Service, Beaufort, North Carolina. The Atlantic coast fishery was considered as a single stock, in keeping with the practice used by the Atlantic Menhaden Management Board (1981), and based on tagging studies by Nicholson (1978). The stock was divided into age groups to eliminate differences in catchability due to age (and size) specific migration patterns.

Calculation of Weekly Abundances

The weekly landings data from Beaufort Laboratory consists of an estimate of the number of fish caught in each age group. Weeks are defined in terms of Primary Time Units, or PTU's. A PTU is a seven day period (Sunday through Saturday) which ends within a given range of dates (see table 1).

Virtual Population Analysis (VPA) was used to obtain estimates of abundance at the beginning of each week for each age group. This method involves using the solution to the catch equation developed by Murphy (1965), and modified by Tomlinson (1970). Tomlinson's method, which is incorporated in the FORTRAN program MURPHY (Abramson 1971),



allows time intervals of unequal length and intervals with zero catches, provided that such zero catch intervals are not consecutive. I further modified Tomlinson's method so that consecutive intervals with zero catches are allowed (see Appendix B). This was necessary because I wished to maintain constant time intervals of one week, to conform to the Beaufort Laboratory's system of PTU's. 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.

In addition to catch by age data, VPA requires estimates of instantaneous natural mortality (M) for all time intervals and an estimate of instantaneous fishing mortality (F) for one time interval. Natural mortality was assumed constant and a weekly value of .0087 was adopted based on the recommendation of the Beaufort Laboratory; thus the assumed annual natural mortality rate was 0.45. Estimates of F for the final week of landings data in each year were obtained from Table 13 of Broadhead et al. (1980) for the years 1968 - 1976 and for age groups 0 - 5. For age groups 6 - 8 the values for age 5 were used. For the years 1977 - 1982, the average values for the years 1968 - 1976for each age group were used (1968 - 1975 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, and M was divided by 53 to

account for the 53 PTU's in the Beaufort Laboratory's system of standard weeks. Instantaneous fishing mortality values were probably overestimated since 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, though it may result in the underestimation of abundance toward the end.

Defining Effort

An index of fishing effort is needed to calculate a catchability coefficient. Effort in the menhaden purse seine fishery is difficult to define due to changes in the fishing gear and methods over the years, and differences in the sizes and types of vessels (Nicholson 1971a).

The vessel-week (number of vessel landings per week) is commonly used as the unit of fishing effort in studies of the menhaden purse-seine fishery, and is the unit used in this study. With this definition of effort, a potential problem exists, in that menhaden plant records do not indicate whether a catch represents one or more days fishing. Vessels generally land their catch daily, but in the Middle and North Atlantic areas they may land two or three days catch at one time, particularly in late spring and early fall. However, menhaden vessels generally operate continuously throughout all or part of the fishing season and fish every day that the weather permits, unless 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. Further, while the number of days that a given vessel was fishing is unknown it was assumed that such variations are fairly consistent from year to year, making between year comparisons possible.

Calculation of Weekly Catchability Coefficients

The catchability coefficient is the fraction of a fish stock which is caught by a defined unit of fishing effort (Ricker 1975). Paloheimo and Dickie (1964) mathematically describe the relationship between catch, effort, abundance, and catchability as:

$$(C/f)_{t} = q_{t}N_{t} \tag{1}$$

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

Since VPA estimates abundance at the beginning of a time period, average abundance in a period is $(N_t + N_{t+1})/2$. Average catch per unit effort in a time period can be calculated as total catch divided by total effort for that period. The above equation can be rearranged to define the catchability coefficient as:

$$q_{t} = (C_{t}/f_{t}) / ((N_{t} + N_{t+1})/2)$$
(2)

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, since the average abundance during the week $(N_t+N_{t+1}/2)$ was used to estimate catchability.

Initial Analysis of Weekly Catchability

Plots of weekly catchability were created for each age group. These plots were visually examined for signs of fluctuation within a season. In cases of obvious fluctuation, it was deemed unnessessary to statistically verify that the fluctuation existed, only to test whether the pattern was consistent from year to year.

The relative degree of weekly fluctuations from year to year may vary due to biotic or abiotic factors. Thus, heterogeneity of variance between years may be expected, and a nonparametric model is appropriate to test for significant difference in annual patterns of weekly catchability coefficients (q). Friedman's method for randomized blocks (Sokal and Rohlf 1981) is the nonparametric analog to the parametric ANOVA, randomized complete block design, but the rankings of the variates within each block are used rather than the actual measurements, and a chi-square statistic is computed rather than an F statistic. The "k" related samples in the study are the 15 years, 1968 - 1982, for which weekly q estimates are available. The q values in different years are related to each other by the week for which they were calculated.

Friedman's test was used to assess the significance of age specific annual variation in weekly q for age groups O through 6. Ages 7 and 8, as well as some years for ages O, 5, and 6, were excluded from the analysis because of insufficient data. Where significant differences were found between years at the 0.05 alpha level, a non-parametric multiple comparisons test based on Friedman's rank sums (Hollander and Wolfe 1973) was used to identify differences.

Calculation of Catchability-Abundance Relationship

Schaaf (1975) demonstrated an inverse curvilinear relationship between catchability and abundance of the type: $q = aN^{-b}$ (3)

where q = catchability coefficient, N = abundance, and a,b = parameters. This equation can be linearized by expressing the abscissa and ordinate values in logarithms. The equation used herein to calculate the catchability-abundance relationship for each age and year for which there were data was

$$\ln(q) = \ln(a) - b*\ln(N)$$
 (4)

where In indicates Naperian (natural) logarithms. Correlation coefficients between the natural log values of catchability and abundance were also calculated for each age group. Only catchability and abundance values drawn from the middle of each season were used to calculate the parameters. This procedure eliminated possible errors in estimation of abundance and catchability due to incomplete availability at the beginning and end of the season. The weeks to be included in each calculation were determined arbitrarily by visually examining graphs of catchability vs. week for each age and year, and selecting those weeks which appeared to fall between catchability spikes caused by possible underestimation of abundance.

Analysis of Catchability Residuals, After Adjusting for Abundance

Residuals of the weekly catchability coefficients were generated by calculating catchability coefficients according to the abundance relationship, and subtracting these values from the catchability coefficients estimated from the catch and efffort data. These residuals were also examined using the Friedman test.

RESULTS

Weekly abundance estimates were made using VPA in each year from the first week in which a catch was landed until the last (tables 2-10). Weeks within this range for which no catch was reported were dealt with as described in appendix B dealing with my modification to Tomlinson's method of VPA.

Catchability coefficients (tables 11-19) and catchability residuals consisting of the catchability coefficient minus the value predicted from equation 3 (tables 21-29) were estimated for each week for which there were abundance estimates for the current and subsequent weeks, except for weeks in which no catch was landed for the age group considered.

The calculated values of the parameters used in equation 3 decreased as age increased (table 20). Because of the large coefficients used for age 0, many of the residuals for this age group were beyond the range allowed by the VAX 11/780 computer, and were therefore not included in the table.

Within Season Fluctuations

The weekly catchability for each age group and year was plotted. Pooled averages for each age group were also plotted to show representative patterns of fluctuation

(figures 1 - 4). The graphs of weekly catchability appear to show a within year pattern in catchability. The first part of the catchability curve features an initial peak followed by a rapid decline. The height of this initial peak relative to the rest of the plot is most pronounced in the age 1 and age 2 fish. It becomes less pronounced and disappears altogether as the fish become older. This first peak does not occur in age 0 menhaden, which are subject to a fishery largely directed against them in the fall.

During the middle of the season, the catchability coefficient is gradually rising with time. If the menhaden stock is assumed to be at full availability during this time, then the abundance of each age group will be decreasing due to fishing and natural mortality.

Toward the end of the season, the catchability coefficient once again rises to a peak, sometimes followed by a sharp decline to zero.

The graph of the age 0 catchability coefficient is different from the other age groups. It remains at or near zero for most of the season, since no age zero 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.

Tests of Hypothesis

The Friedman tests for the hypothesis of no significant differences in the pattern of catchability coefficient fluctuations between years indicated that there was at least one year which was significantly different from the others at the 0.05 alpha level for age groups 1, 2, 3, and 4 (table 30). These are also the only age groups for which sufficient data are available to include all 15 years; conversely, those age groups showing no significant differences between years (age groups 0, 5, and 6) were also those with fewer data to work with. Subsequent multiple comparisons for age groups showing significant differences between years (figure 5) showed that years which were not significantly different could be placed into two or three groups. However, no inferences could be drawn from the pattern of groupings.

After subtracting catchability due to abundance, the Friedman test was run on the residuals (table 31). All age groups, with the exception of age 5, showed significant differences. Neither the test probabilities nor the rankings of h e years in the multiple comparisons bar diagrams (figure 6) showed much change.

A week negative correlation was found between ln(q) and ln(N) for each age group, with data from all years pooled (table 32). Values ranged from -0.161 to -0.325 for age groups containing more than 100 data points. The correlation coefficient decreased toward -1.00 with increasing age, except for age 3. However, the number of data points used to calculate the correlation coefficients also decreased with increasing age.

DISCUSSION

The weak negative correlation between abundance and catchability indicates that abundance is not an overiding factor governing fluctuations in catchability. However, since a correlation, although weak, does exist, taking abundance into consideration may improve the accuracy in estimates of catchability, and enhance assessments which utilize the catchability coefficient.

For example, one method of estimating fishing mortality is from:

$$F = qf$$
 (5)

where F = instantaneous fishing mortality, q = catchabilitycoefficient, and f = fishing effort. This assumes that fishing mortality is proportional to effort, where q is constant. However, a simple substitution for q by it's abundance relationship, aN^{-b} (Schaaf 1975), gives:

$$F = aN^{-D}f$$
 (6)

While this equation requires estimates of abundance as well as effort, it permits catchability, and therefore fishing mortality, to vary with abundance, and more accurately estimates F during the fishing year as population abundance declines due to both natural and fishing mortality.

Within Season Variation

The First Peak - an Availability Anomaly

The existence of this initial peak is probably due to underestimation of abundance at the beginning of the season as a result of the VPA method used. Virtual population analysis measures the "virtual" abundance, that which appears to the fishery to be there. Very 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. This availability, or accessibility, causes a measurable modification in the catchability coefficient (Cushing 1968). Marr (1951) showed that catchability is directly related to availability. However, VPA assumes that there is full availability, thus abundance is underestimated. Several researchers have demonstrated an inverse relationship between abundance and catchability (Smith 1944, Palcheimo and Dickie 1964, Pope and Garrod 1975, Schaaf 1975, Ulltang 1976, Garrod 1977, Peterman and Steer 1981). Shardlow and Hilborn (1985) demonstrated that if the abundance is underestimated, then the catchability coefficient will be overestimated.

Theoretically, this first peak should extend up to infinity prior to the start of the season when VPA is used to estimate abundance. Had abundance been measured using a method independent of the fishery catch statistics, such as mark-recapture, the catchability coefficient would be expected to rise from zero without an early season peak, unless caused by other factors. This 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 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, then VFA will not underestimate abundance, and consequently catchability will not be overestimated. One advantage of examining within season fluctuations of catchability, therefore, may be to determine how quickly and at what point in time a stock becomes available to the fishery.

The Middle Section - an Inverse Abundance Relationship

Schaaf (1975) reported a logarithmic inverse relationship between catchability and abundance of menhaden. This is a likely explanation for the gradual rise in catchability noted in this study during this period. An increase in this rate might be an indicator of overfishing.

The End Peak - another Availability Anomaly

As with the first peak, this peak may be due to underestimation of abundance by VPA due to decreasing availability of the menhaden as they leave the fishing grounds. Age 0 - a Directed Effort Effect

Age O menhaden are fished extensively in the North Carolina fall fishery which is largely directed toward these fish. The pattern of catchability for age 0 menhaden differs from that of the other age groups in that fishing effort is specifically directed toward these fish at certain times. Paloheimo and Dickie (1964) state that when fishermen selectively apply their effort toward some schools, the result is to vary the catchability coefficient depending on age, species, and relative abundance. This effect is apparrent in the plot of average weekly catchability coefficient for age 0 menhaden, which is guite different from the plots of older age groups. When the age O 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.
SUMMARY

Several age groups showed significant differences in catchability fluctuation between years. After calculating the relationship between catchability coefficient and abundance and subtracting catchability due to abundance from the total catchability, the residuals also showed significant differences between years for all but one age group. The correlation coefficients for age groups for which there were large amounts of data ranged from -0.161 to -0.325. It appears that density dependence is not a major cause of fluctuation in the catchability coefficient, but does explain some of the variation.

The catchability of Atlantic menhaden does not remain constant. There are fluctuations in the weekly catchability coefficient over the course of a year. Taking these fluctuations into consideration may enhance assessments which utilize the catchability coefficient, and result in more accurate estimates of fishing mortality.

The gradual rise in catchability in the middle section of most catchability plots can probably be attributed to a gradual decrease in stock abundance due to fishing and natural mortality. A departure from "normal" in this section of the catchability plot might be used to indicate the existence of over or under fishing on a given age group

and year.

A directed effort on a particular age group will result in a different pattern of catchability fluctuations compared with other age groups. Although in the case of Atlantic menhaden this pattern is also readily apparent in the catch statistics, it may be possible to use this in other fisheries to indicate a directed effort when the catch data alone are more ambiguous. A directed effort effect may also occur when economic conditions favor menhaden over alternative resources.

Changes in migration patterns and behavior of Atlantic menhaden may result in changes in the pattern of catchability coefficients. If the menhaden behavior changes in response to environmental conditions, then changes in the catchability plot may be an indicator of changes in environmental factors. Conversely, if a relationship between an environmental factor and catchability can be established, then this knowledge can be used to account for some of the variablity of the catchability.

APPENDIX A

What is Catchability?

Catchability is the fraction of a fish stock which is caught by a defined unit of the fishing effort (Ricker 1975). It is a measure of how likely fish (or any exploited organisms) in a given stock are to be caught by a particular type of fishing gear.

Catchability is different for each combination of stock and fishing gear. Thus, the catchability of a stock being fished by purse seiners is different than the catchability of the same stock being fished by trawlers. Two different stocks fished by the same type of gear might have different catchabilities even if the stocks are of the same species. This could be due to biological differences between the stocks, such as different growth rates. For example, Brauhn and Kincaid (1982) found significant differences in the catchabilities of different strains and families of rainbow trout which were reared under identical conditions and fished simultaneously from the same pond. Strains were identified on the basis of differing growth rates, and families by individual ancestry.

Even for a specific type of fishing gear, differences in catchability can exist between individual pieces of gear. Differences between operating characteristics of the boats,

experience of the fishermen, and changes in material, construction, or the method of using the fishing gear can all contribute to differences in the gear efficiency, which affects catchability. When a fishing fleet consists of several pieces of gear, the catchability and gear efficiency for the fishery is the average of the individual pieces of gear. Small random changes by the individual fishermen are unlikely to have a significant effect on catchability for the fleet. However, changes by several of the fishermen, such as would happen when improved gear or methods become available, will cause a long-term trend in catchability.

Literature often refers to availablility rather than catchability. Availability is the degree to which a population is accessible to the efforts of a fishery (Marr 1951). Catchability is a function of availability and gear efficiency (which is assumed constant), i.e.;

$$q = kr$$
(1)

where q = catchability coefficient
k = constant representing gear efficiency
r = availability, the fraction of the
population available to the fishery

In the remainder of this discussion it will be assumed that only one type of gear is being considered. Therefore catchability and availability will differ only by the product of the constant k. Their variabilities will be related, the variance of q being equal to the variance of r times k^2 .

Types of Variation in Catchability

Although catchability is usually assumed to be constant, it is actually subject to variation. The causes of these variations can be divided into five general categories.

1) Cyclical Changes in Catchability

In many fisheries a cyclical variation in catchability exists due to seasonal changes in fish behavior or distribution (Gulland 1964, 1969, Pope and Garrod 1975). Such changes may be the result of cyclic environmental conditions such as temperature or length of day.

Pope and Garrod (1975) show a significant change in catchability between quarters for various cod fisheries. Gulland (1964) reported that the CPUE of Arctic cod is at a minimum in the Autumn, and that in many herring fisheries and other seasonal fisheries, the CPUE is nearly zero outside the fishing season. Although Gulland (1964, 1969) felt that seasonal fluctuations are unlikely to cause serious errors when estimating annual mortality or abundance, Pope and Garrod (1975) state that a knowledge of seasonal change in catchability could be used to reduce the variance of catchability, which plays a major role in causing analytical errors in the objectives of management by catch and effort regulation. A knowledge of seasonal variation might also be used to investigate the effects of intra-seasonal management options such as changing the opening or closing dates of a fishing season, which are likely to be periods of rapidly changing catchability, or of having a split season, which would stop fishing during a period of relatively stable catchability.

Other short-term cycles may also exist. Staples and Vance (1979) found a marked tidal periodicity in the catchability of juvenile and adolescent banana prawns, <u>Penaeus merguiensis</u>. Morrissy and Caputi (1981) reported that variation in catchability of freshwater crayfish, marron (<u>Cherax tenuimanus</u>) is associated with underwater illuminance and moon phase. Such fluctuations are unlikely to be significant when examining catchability on a seasonal or longer term basis.

2) Long-term Trends

Long-term trends in catchability may be caused either by increases in fishing power or by biological changes. Such trends are usually the result of improvements in gear or fishing methods (Gulland 1964), but in many fisheries this conclusion may be questionable. The Atlantic menhaden fishery has shown a consistent increase in catchability with time. This increase has been attributed to an increase in gear efficiency (Broadhead et al. 1980), but Schaaf (1979) reported that the increase in gear efficiency since 1960 is the result of a decline in population size.

Pope and Garrod (1975) reported that the estimated catchability of Arcto-Norwegian cod for Norwegian fishermen has shown a steady increase over time, but it was not clear how much of the increase was due to increased fishing power and how much to biological change. The same stocks showed no long-term trend for the UK, USSR, or Federal Republic of Germany fishing fleets.

For the West Greenland cod stocks, Pope and Garrod (1975) reported an increase in catchability with time for all fishing fleets. This increase had been previously attributed to improved efficiency of trawls. However, Pope and Garrod noted that the catchability estimates for Portuguese dory vessels show the same trend. Since dory effort measurements exclude increases in fishing power of the mother ship, they concluded that the increase in catchability was due not to increases in fishing power, but to changes in the availability of the Greenland cod stock.

3) Density-dependent Changes

Schaaf (1975) considered fisheries to be a type of predator-prey interaction, and discussed the effect on ecosystem stability and mangement decisions of three types of relationships between catchability and abundance; catchability constant, catchability varying directly with abundance, and catchability varying inversely with abundance.

Constant catchability contributes neither stability nor instability to the system, and results in a linear relationship between CPUE and effort.

Catchability varying directly with abundance tends to stabilize a system. As abundance diminishes, so does catchability, and it becomes harder to catch members of a population. Thus, tight restrictions on catch or fishing effort are not necessary to maintain an equilibrium yield close to maximum.

Catchability varying inversely with abundance tends to destabilize a system. As abundance decreases, the proportion of the population caught by one unit of effort increases, and tight restrictions on catch or fishing effort become necessary to maintain an equilibrium yield.

MacCall (1975) found that the catchability coefficient for the Pacific sardine purse seine fishery was inversely related to abundance along a logarithmic curve.

Ulltang (1976) reported that in many purse seine fisheries, such as the Norwegian fishery for capelin in the Barents Sea, a fleet may be able to follow concentrations of fish for a long period. If the density of the school does not decrease significantly with decreasing stock size, then the proportion of fish caught by each unit of fishing effort will increase. Ulltang found that for the Norwegian purse seine fishery on spring spawning herring, catchability was inversely related to stock size logarithmically.

Schaaf (1975) found that the behavior of menhaden, which school densely and are visible from spotter planes, results in a logarithmic inverse relationship between catchability and abundance. Similar inverse relationships between catchability and abundance have been found for chinook salmon (Peterman and Steer 1981) and North Atlantic cod (Pope and Garrod 1975, Garrod 1977).

4) Density-independent changes

Density-independent changes in catchability may be caused by changes in behavior or distribution brought about by environmental fluctuations or biological changes. Morrissy and Caputi (1981) reported catchability of marron in baited drop nets to be associated with size, sex, female spawning activity, moult stage, and previous history of capture, in addition to the cyclic variables mentioned previously.

Farman et al. (1982) reported that catchability of largemouth bass in Back Bay, Virginia tournament angling was associated with water temperature, transparency and salinity.

For menhaden, Reintjes and Pacheco (1966) theorized that behavior and distribution could be affected by physical factors such as waves, currents, and turbidity, and by chemical factors such as oxygen, carbon dioxide, hydrogen sulfide, hydrogen-ion concentration, inorganic salts, and organic compounds.

5) Changes Due to Changes in Fishing Effort

Changes in catchability due to changes in fishing effort are not very common (Gulland 1964). Such changes can occur when the fishing is so intense that one piece of fishing gear interferes with another. Situations of this type might occur, for example, if gill nets are set too close together or if several purse seiners are converging on the same school or patch of fish. Gill nets and long-line fisheries may also have changes in the catchability as a result of decreased efficiency due to gear saturation (Garrod 1964).

Changes in catchability can occur as a result of a fishing fleet changing its location and distribution to concentrate on areas where the fish are most abundant (Gulland 1955). When fishermen are able to selectively apply their effort toward some schools while avoiding others, perhaps to select the schools giving maximum economic return, the result is to vary the catchability coefficient depending on age, species, and relative abundance (Paloheimo and Dickie 1964).

It is also possible that intensive fishing may change the behavior of the fish, such as breaking up the shoals of schooling fish (Gulland 1964). Nicholson (1972) reported that fishing intensity above a certain level appears to decrease the availability of menhaden to purse seines. He suggested that high fishing intensity might affect the mechanisms by which small schools coalesce into larger ones, or that it might make fish "wild", so that schools sound when vessels approach.

APPENDIX B

EXTENDING TOMLINSON'S GENERALIZED MURPHY CATCH EQUATION TO INCLUDE CONSECUTIVE ZERO'S

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 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 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 two or more consecutive zero's do not occur.

The normal method of insuring that consecutive zero's do not occur in the catch data is to pool time intervals containing zero catches with adjacent non-zero intervals. In some applications involving computer analysis of the results or comparisons among several sets of catch data, it may be desirable to keep the time intervals fixed, even if

this results in consecutive zero's in the catch data. This paper will extend Tomlinson's concepts to allow for any number of consecutive zero's, provided that the first and last time intervals contain catches. The notation used follows that of Tomlinson (1970).

Equations 1 through 5, along with the accompanying explanations, are from Tomlinson (1970) and are reproduced here to provide a review of his model, upon which this extension is based:

If N_i is the number of fish in the cohort alive to begin interval i, then the number alive to begin interval i+1 is given by

$$N_{i+1} = N_i e^{\left(-t_i (F_i + M_i)\right)}$$
(1)

The catch in interval i is given by

 $C_{i} = N_{i}E_{i}$ $E = \frac{F_{i}(1-e^{(-t_{i}F_{i}+M_{i}))}}{F_{i}+M_{i}}$ (2)

The catch in interval i+1 is given by

$$C_{i+1} = N_{i}e^{\begin{pmatrix} -t_{i}(F_{i} + M_{i}) \end{pmatrix}} E_{i+1}$$
(3)

A catch ratio (R_i) can be constructed for all but the last time interval. The ratio for interval i is given by

$$R_{i} = \frac{C_{i+1}}{C_{i}} = \frac{e}{C_{i+1}} = \frac{E_{i+1}}{E_{i}}$$
(4)

If $C_{i+1} = 0$, then $E_{i+1} = 0$ and $r_{i+1} = 0$. In this latter case

$$R_{i+1} = \frac{C_{i+2}}{C_{i}} = \frac{e}{\frac{C_{i+2}}{C_{i}}} = \frac{e}{\frac{C_{i+2}}{C_{i}}} = \frac{e}{\frac{C_{i+2}}{C_{i}}} = \frac{e}{\frac{C_{i+2}}{C_{i}}}$$
(5)

Extensions to Tomlinson's Model

A generalized form of the catch ratio between any two time intervals, where the catches for all intermediate time intervals is zero, is

$$C_{i+k} = E_{i+k} e^{-t_{i}(F_{i}+M_{i+1})-t_{i+1}(M_{i+1})-\cdots-t_{i+k-1}(M_{i+k-1})} E_{i}$$
(6)

The Forward Solution

The forward solution involves estimating E_{i+1} from E_i or from E_{i-k} . If $C_{i+1} = 0$, then E_{i+1} and $F_{i+1} = 0$ also. When $C_{i+1} \neq 0$, find the nearest non-zero E_{i-k} , where k has a value of 0 or larger. The catch ratio needed for this estimation is C_{i+1}/C_{i-k} . By substituting the value L = i-k,

$$C_{i+1} = C_{L+k+1} = \frac{C_{L+k+1}}{C_{L-k}} = \frac{E_{L+k+1}e}{E_{L-k+1}e}$$

$$C_{L-k} = \frac{C_{L+k+1}e}{C_{L}} = \frac{E_{L+k+1}e}{E_{L-k+1}e}$$

$$(7)$$

Rearranging the above equation to solve for E_{i+1} and substituting back i-k for L results in

$$E_{i+1} = \frac{C_{i+1}E_{i-k}e^{t_{i-k}(F_{i-k}+M_{i-k})+t_{i-k+1}(M_{i-k+1})+\dots+t_{i}(M_{i})}{C_{i-k}}$$
(8)

Once the array [E] is known, the array [F] may be found by iteration from the following equation (Tomlinson 1970, eq. 7):

$$E_{i} = \frac{F_{i}(1-e_{i} + M_{i})}{F_{i} + M_{i}}$$
(9)

The Backward Solution

The backward solution involves estimating the value of $E_i \exp[t_i(F_i + M_i)]$. This can be estimated from E_{i+k} by rearranging equation 6 as

$$E e_{i}^{t_{i}(F_{i}^{+} M_{i})} = \frac{C_{i}E_{i+k}e^{-t_{i+1}(M_{i+1})-\dots-t_{i+k-1}(M_{i+k-1})}}{C_{i+k}}$$
(10)

where $C_{i} \neq 0$, and all catches between C_{i} and $C_{i+k} = 0$. F may be found by iteration of the following equation

(Tomlinson 1970, eq. 9)

$$E_{i}e^{t_{i}(F_{i}+M_{i})} = \frac{F_{i}(e^{t_{i}(F_{i}+M_{i})}-1)}{F_{i}+M_{i}}$$
(11)

Once F is estimated, E can be estimated by

(The value of
$$E_i e^{t_i (F_i + M_i)}$$
)
 $E_i = \frac{t_i (F_i + M_i)}{e^{t_i (F_i + M_i)}}$ (12)

Once the arrays [E] and [F] are known, whether by forward or backward solution, the population size at the start of each time interval can be estimated from

$$N_{i} = \bar{E}_{i}^{i} \quad \text{where } E \neq 0 \quad (13)$$

or from equation 1.

A computer program, MURPHY, is available in Abramson (1971) to solve for population estimates, fishing mortalities, and exploitation rates using Tomlinson's model. A modified version of this program, VPAMOD, incorporating the extension for consecutive zero's was prepared to estimate weekly abundance and fishing mortalities for the Atlantic menhaden paurse seine fishery. The catch data were broken up into seasons and age groups within a season. For those data sets which do not contain consecutive zero's, and thus can be analyzed by MURPHY, the results obtained from MURPHY and from VPAMOD were identical.

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РТU	Week From	Ending To	PTU	Week From	Ending To
1	3/01	3/07	27	8/30	9/05
2	3/08	3/14	28	9/06	9/12
3	3/15	3/21	29	9/13	9/19
4	3/22	3/28	30	9/20	9/26
5	3/29	4/04	31	9/27	10/03
б	4/05	4/11	32	10/04	10/10
7	4/12	4/18	33	10/11	10/17
8	4/19	4/25	34	10/18	10/24
9	4/26	5/02	35	10/25	10/31
10	5/03	5/09	36	11/01	11/07
11	5/10	5/16	37	11/08	11/14
12	5/17	5/23	38	11/15	11/21
13	5/24	5/30	39	11/22	11/28
14	5/31	6/06	40	11/29	12/05
15	6/07	6/13	41	12/06	12/12
16	6/14	6/20	42	12/13	12/19
17	6/21	6/27	43	12/20	12/26
18	6/28	7/04	44	12/27	*13/02
19	7/05	7/11	45	*13/03	*13/09
20	7/12	7/18	46	*13/10	*13/16
21	7/19	7/25	47	*13/17	*13/23
22	7/26	8/01	48	*13/24	*13/30
23	8/02	8/08	49	*13/31	*14/06
24	8/09	8/15	50	*14/07	*14/13
25	8/16	8/22	51	*14/14	*14/20
26	8/23	8/29	52	*14/21	*14/27
			53	*14/28	*14/29
*Months	13 an	d 14 refer to Jar	uary and Febru	ary of	the

Table 1.	Conversion	dates	for	Primary	Time	Units	(PTU)

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Table 3. Abundance Estimates for Age 1

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Table 8. Aburdance Estimates for Age 6







Table 10. Abundance Estimates for Age 8



Table 11. Meskiy Catchability Estimates for Age D

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Table 13. Newskiy Catchebility Estimates for Age 2

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Table 14. Neekly Catchability Extinutes for Aga 3

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		16863/10280	19525004	INTERIOR.	Number of the local division of the local di	11854.1000	DODEFTRO	184212328-	10011125	11233000	142262800	80302000	12232000	08815200	INFUSCION .	SICHADOR.	161202000	105122302.	10000000	NEDCENSO.	57296260	PARTICIPAL D	111 196 995	000012794	36826577	linizinis"	-		1				-			-	-	
2			10022100	129121000	Tablinka.	BUCKERSON.	109011000	198712005	10016354	IT200000	Isoccost.	191222060	05122000	SCHUTCHING .	10010100	NCRECOOK.	1250623007	BC122060"	#1.58200t	0031254	19851040	Ches the	101102386	MODITHEN!	DIDDENLA	1981 1984	HEIGHOOD.		CONTRACTOR.	TADALALA.	001962511	I I BLINDING'	-		-		-	
ŝ		SETADOOL.		CLUMBER -	1111111111111	19651000	CLUSION.	11251 1000	MAN LANK	00001136	.00005146	EGENIDOD.	11101000	NET RECOOL	1001010	1411200	23023000	00019427	90055275	51786000	METS DADO.	PART 1944	1000000	00447310		100011688	-	51519000	CARLY OWNER.	and in 2 hours -		-						
5	Sastaote	ATELOOOT.	SC20000.	1000114650	BARCOON.	Consider.	MEN12940.	00074686	COLUMN .	CENT2005.	.00004473	10025488	C SOULDON-	100001000	IL STANDOL	1000545148	0006134	Pateroon.	SHLIDOOD'	L'ETERADO.	Including to the second	00011000	TRADOCTARIA	100685128		1221 20060	COUNTRY OF			10111110	001223479					_		
5				MARCHES .	111922000	POST STORE	GHL88000-	10011504	00628440	108512000	MIN21000	21282000	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	10143000	D0000396	00021458	.00045680	LISCHCODE-	111122 0000	28811000	TRADING.	20077451	190181360	11987-2000.	Hattagoon"	00000031	DODUTIESS	AAN TAKE	TANKARTON.			-	-			-	-	
6				_	ACOUNTAL	CAL 50000.	ST811000	THE NUMBER	20000000	R 51 20000	E340000	ACHSCOOL	BU MU DOD	100010001	00010057	112101010	55580000	50150000	28060000	SCINDING.	TANKING .	201000	0001342wl	A4012120	BELINLOOD.	101000001		_	BERENOU.		_	-			_	-		
6					1	123593007	000142K3(100121000-	10000000	Add Sans	144512000	144794020	CALCULARY OF A	PSC WEDDING	00010963	13121000	000485800	DODTSA12	11111111111	110101000	The state of the s	CLENING D	00007906	A118128	100020359-	198663980	ACRESIONS.							-	~	-		
	1001100	-			69080363	002390002	HCOLDOOD"	LAUTION	13521-0000	00239522	ESERVICO.	101112000	CONCESS.	100118281	10038000	00045506	118812000	20212000	- PUDBA132	ATTACATA	TATA STORE	124213451	1090120001	00190199	12652900	199952908	HESELADO.	17771.344		1	11111111111				-	-		
		~	-		COCDUDAA)	18513830	0610000	- D0030718	100222002	100355689	00011000	WEDGE ST	STATISTICS IN	Tau Causa	BU222000-	123325002	10081824	96212090	Ganzana.	STATISTICS.	1.85	COLDNESS	10055120	MANS ISA		C8055852	116210.000	and a state of	CODINE AND						-	-		-
8				00000436	21211000	SUMALISA	B0001000-	BURNING AND	CONTRACTOR	90022615	101201020	01022000	ANALYSIA .	231.93000	B1219000"	C0048921	00058010	12312001	22042.894	TAN BURN	INCOME.	DDR7544	2001/055	00072297	1225200	00183012					_	_			-	_		
		MILLOSON-	-00000146	121600001	.0000866K	0122368	BLIDGOOD-	TAXABLEDO'	TABAGAG	AND NOT ADD A	129051000	12012000	Distancial in	BAZRESSES	10662000-	00022808	SCHOOLOGO.	Lisztnier-	Talai tang	100000	10000000	3277 1084.	(SENCIED.	I steers into	2121 4080	20101200	TOTAL AND ADDRESS OF TAXABLE PARTY OF TA	000000		-		-		-	-	-		
				10001352	11540800	21212200	#50×2000*	LOLDING.	antistres.	24210000-	25982000	12420000	Manual Annual Annua	12122000	00004311	1672594	21193000	LZ I DOUGT	1.7741.010	00001855	12010100	00045344	100012000	1000002112	142111000	Taxable Contraction	TING TING	00047001	20065135	100121002	PARTICULO.					- •		
			100011000	MELET 000.	SELECTOR	116112000	VENUDADA.	PAAL DATE IN COLUMN	0001001	12101007	Linkstown-	11.10000	152880090	00014172	(nastrood).	120580000	100001468	AND DOOL	1 Statements	112300000	00020894	90052598	000630511	114883900	119112000-		TARGET I	-000T046E		LL PISORD	130324226			-	1	+		
	CLARKS B	5086233	ACC2000	1011251	0972790	12231-00	COLUMN TWO	SALES OF	1195000	111114	0026543	2622624	2138225	0023183	9021925	0017204	10111256	12121120	Constant of the local division of the local	C010514	OCTOR N	68(5183	1519100	BU2K2ES	1011111	19622100	ALL	8225148	0153223	-	-			-				

Table 15. Meekly Catchability Eatlantes for Age 4

	States and	107 1054020 107 1054020 107 1054020	10 SCREEK		ECONOMIA	IL REPORT	SACOSIO	44
		A PROPERTY AND A PROP	I ISBNI	0. (195510 0. (195510 0. (195510	0. 1989000 0. 1971200 0. 1971200	0 1995010 0 1995010 0 1995010		642.000 642.000
		64- 100- 1516 100- 1516	00 Sac	007 1521	007 1000 007 1000 000 1001	100 000 000 000 000 000 000 000 000 000	100 100 100 100 100 100 100 100 100 100	1000 1000 1000 1000 1000 1000
1111		100 1000	1000- 111	100 - 100 -	10000° 144	1000 100 1000 100 1000 100		1000
	B17500	80.000 NG2000	N2000.	192000	200000. 1745260 12628600.	815000. 120000.	121000 200000 200000	HI SSECO
101	863 N2 1-00 -	12812000 212942000	RACCOM.	10010000- 100000000-	1000000	A2538000-	N252000 N3401100 R2112000 R2112000	NJ 5538000 *
		CREECING.	RECTION.	NCHIM	559651.00	Cerissee'	54551 200.	
		12842000	BURGERAND.	SCHUDD	112842800	ACCESSOR.		
			ametrea	5-54500	128511909.	26224001	190201 MB	
		STTREED.	NTT22000.	94110001	19905000	5364000	-00166157	
	119621000	122890000" 122891000"	125102000"	147420000. 147420000.	INCLEMENT	SELENDO	151211000" 123512000" 1215520100"	
	141128000	1635240000 1238624000	CT801000.	11855300	LLSLIGHT	Numeron and a second	135122100 13512100 14512200 192888000 192888000	55152100
		e1200000	22395000	CORPORAD.	6C810000	56282000	lessure.	
	action.	ALCORDO	A REALING	14521-140"	BC21000		512381000"	18×C57140.
	LANKSAD	1001210	12111100	NCSARSAN SINGSARSAN SINGSARSAN SINGSARSAN SINGSARSAN	11111111111111111111111111111111111111	C122200	N23510	10020400

Table 18. Meekly Catchability Estimates for Age 5

and a	Representation Repres
1 1881	121191007 12119200 12119000 1211900 1211900 1211900 1211900 1211900 1211900 1211900 1211900 12119000 12119000 12119000 12119000 12119000 12119000 12119000 12119000 12119000 121190000 121190000 121190000 121190000000000
1481	1.1422400 1.142400 1.1424000 1.1424000 1.1424000 1.1424000 1.14240000 1.14240000 1.14240000 1.142400000 1.14240000000000000000000000000000000000
6281	22232000 100607000 100607000 100607000 100607000
1978	ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION. ELATION.
187	128613000. 17282011000. 1728201000. 17282000. 17282000. 17282000. 17282000.
1416 I	
1815	
1 101	IENessoon Screesoon Screesoon
1111	3 121 M000 1 21 0000 1 21 00000 1 21 000000 1 21 00000 1 21 000000 1 21 00000 1 2
1177	TREFFROM. TREFROM. TREFFROM. T
1 1181	LLX81000 LLX81000 LLX81000 LLX81000 LLX81000 SSEL2000
1 1011	EC256100.
1 1981	8551 M00" 8551 M00" 8551 M00" 8551 M00" 8551 M00" 8551 M00"
1 1981	LISAL0000 LISAL0000 LISAL0000 LISAL0000 LISAL0000 LISAL0000 LISAL0000 LISAL0000 LISAL000 LISA
E.	
Table 18. Neekly Catchability Estimates for Age 1



Table 11. Neekly Catchability Estimates for Age I



Age	ln(a)	b
0	5814.75146	260.73114
1	13.64552	1.07412
2	-4.78667	0.14681
з	-6.63207	0.08351
4	-7.28095	0.04313
5	-7.49682	0.02430
6	-7.24914	0.00326
7	-4.63377	0.00027
8	-10.12862	0.00032

TABLE	20.	Coefficients	Used in	the	Catcha	abi	.1i	ty-Abundance
		Relationship:	ln(q)	= 1	n(a) -	b	*	ln(N)

fable 21. Meekly Catchability Entimates for Age 0 Adjusted for Abundance



Table 22. Heekly Catchebility Estimates for Age 1 Adjusted for Abundance

	08912007	UR352800-	*1080100	-period Stan	21 Ectant	CI640007 -	11140404"-	Transformer -	00001001	#0003555	·	+1818000 ···		Polessing.	02.0	CTU COT		0.80	-, 0001101a	*******	-, 00005B4.6	-, 20015214	TTT NOT T	0000005		215521006		ETICO00	Contraction -		201254255	SVILIBUT'-	AL NO TAMAN'-				
		ANTERNA.	BILNUM.	BUNCTRD.	*******			PROPERTY -	chicking.	1412000	600031182	bobs1778	1210000	CELLINGS -	961 State -	*	E11000'-		-, BUTVERS		-,0001315.3	LISELLAN" -	3 (11 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	- 0012.82	E CALCONNY	12030063	- 400012 -	1023-200	61 110 ····	- TDI DUD	- 2002 8 0	16062000				-	_
	Anacom.	MORENAL .	District.		05151000.	MARK THE	9185.309	Traction.	2128.300	\$2001Y582	01511000"	SI B SROND		CICODA.		00003526		Contraction of the local division of the loc	Partitions.	-, 0000135F	000548225	\$1730000°-	CALINDIAN -	MODIFIER .	00110	- ,00039555	A \$4000 -		STATISTICS	With States							
		- 00009273	781	*, D0006161	· . Milling 024	- mmB056	- 400 0596	COMMON -	10000000		- 0002407	\$11 E (04)		250	AND ADDRESS AND ADDRESS ADDRES		POINTING	12021000'-	- 0000000 -	- , 0000008333	Constraint.	- doitase	BULLENOU	ALLINGTON -	ETB12000		- 00016122	-, 00016436	CINDRENO	THE PARTY OF	-, 10034666		12152385-	- HERTYLER			
B	K125-260,	CHUILDEN.	ALTINOTY	MINDOON.	20472943.	-, INDASAS	BELLINGHT.	CODATON,	TOTAL DATA IN	CRIMINA.	0001223	EX825000	00000280	CALCUMPT -	1 100 100 100 -	PROPERTY.	8120000	63622300	1134000	0007520	D000454.0	B4808080'-	9532000	COLUMN TO LO D	20121100	THEORY &	6.222.2000	.000125100								_	
			000101010	10002726	18840881			+-4000 IS	ADD DO TO	- THENGY		- MANAGIN	- 00005076	- 00053+	10000	21000	- 0000 1300	120031	Caracter.	81234049	00002356	DEBODDESS	PROB2446	CLINES -	Montana.	1002001	MULTINE	DOTTING.	DOINSETT	COLUMNS'	\$2361100/~	44012752					
-	15 M542300	Internet.	1110000	- PROTICUL	- 09006371	BBBR2472	B4110607	BACCORD-	- P0022094	The state	BORDON	- ADD25865	STADIO.	10000	- 11000 -		11000000	TI-TOUR		ATLANT'	-, 00004113	-, PROBINES	23118062	ACCREDING.	10020200	1 1 60	10035-01	10029-21	10031598	000000	- 100 L2665						
-		1 10 12000 ***	100001021	Times .	- 66603355	00001541	82514040	\$1474690	C100001943	- 2001 1200		DODAA2955	MCMADO.	10000035	PLANTING -	11 200000	0000033	- 001025m	- 102394	- 01107511	MECOND -	1002000	10001014	21109000 ·	ATTANDA	00100120	00009616	0001054	-, 00004575	115 1000	LACKNEY.	-,00010585					-
-	10,000	SMITTORS.	11220062	101011010	100001	IL NUMBER	SPIELING.	10001246	APPROX 12	a tanua	10000125	3050513	MULTING.	- 9000CN1	SCHOOL ST	ACTORNAL .	74620000	10111181	11923030	EL LANDO	Statistics.	1001136	0000000	20022300	STATES	5448000	20011409		34810000	84110000 -	ALBORITO -						
	CIACHERS.		PRODUCTION	AGREED 15	DODDING T	TACKED .	D000%2+7	NERVICE -		The second secon	1021400		HI610000"	- 10100101-	1901100	Jan 1 and	000 513	- 000 317	115 000	DOC SAA	000 5 5	D001115	000 244	10012000		ALL DO T	Ban Chia	18401000		2 5 5 5 5 5 5	Support -		CONTRACTOR				_
100	PRO 101	. 99103010	Contraction -	1 070	- 1022P4	- 302001975	99400288	- 1 029 1	- 10010	Contractor -	- DOCINE	- DISEBUT		121 MIGHT-+	VIANA PARA	C0002562	.0000273	1001000	- 00011000	1131100	10003376	WARRAND.	- 90902254	BUTNER'-	ALL MODE .	and a lot of the lot o	26012417	10020051	0027544	11 NO1 Dod	20100000 -		\$12×100*				
		-	Property lies	THEMANDY -	Total Links	ANTARANA	1280800		12230001-	Carlander-	ACRESSES.	PACKERS,-	- deserver	C365100-	111111111111	10000001		15541000	E4851000	THURSDAY INC.	10022000	20017036	CONNECT.	211/200	Annual Trans	- 10000	- 000 I BB	02121008	0001#C000		Minister.	CONSIGNA-					-
III		30311506	-000 550 H	a cuta	A PROPERTY AND	20000165		10001	1812000	AND DESCRIPTION OF	60000	0123D	- 101176	AZEED	05500	10010	18281400	.0003545E	.00021252	Distantes.	TTORNAGT	1940004.	22303036		101111111	STATISTICS.	14000000	ACARCERS.	71962000.	00000151	PICTORE -	* MODE 14 *	-,40476201	1220000-	Largenter'.		
181		172411031	NUCODA1436	Table in the local sector	ALCONOM -	-,00001355		**. INDUTING	MODODERT	247 Lason	Station -	00001067	- 40001344	NUCCORDS	1 NO000141	and the state of t	LIEInun -	ALANGOROW.	Discional.	TANK TANK	CONSIGNATION OF THE OWNER OWNER OF THE OWNER OF THE OWNER OF THE OWNER	20200400	ECSNOIDS-	1000000	L MEDICO.	STREET.	00012175	TRACINICAL	SCS #SIDE	00023145	WINNING.						
100			PIONOIO.	ALC: NO.	A REPORT OF		10001231	"BORDBORL-	1000000	CANDING.	STREET, STREET, ST	retelation.	CONNAME.	ENCLOSED.	MONTH.	10210303	190.001	PROTESSION.	papeton 1	ALL DO NO.	10012051	.000000	CHONOLES!	8015000	14142080	100		+, distanti	HOUTED	LOADEDAN" -	SAME NO.						

Table 21. Weekly Catchebility Estimated for Age 2 Adjusted for Abundance

1		- 00111260	31231000-	101100-	STREETS IN	1258112ml	SETZION.	41242000	Contraction of the local division of the loc	No. of the local division of the local divis	10013777	12122120.	OESSIGE"	abutant.	WESSIGN.	N942(0)*	a tableton.	1010101	ACSEMPT.	00012526	PORTONIC	111100001	ALE 1001101	***********	37240000	PODA4851	00846913	TOTAL OF	10011534	- 101504		-	_				
IN		NEWSONAL	S10001	VEHIDIDA.	RESLORD.	10012082	2000394.3		1 133000	STREET,	AEBT 1000.	2002115	213	10163300	-0001000-	#C121060*	- 10000	A ACL MAN	WLEI-CODD"	22032300.	11216300	TITLE STORE	AND CLOSE -	ILS NOV	STATUDA.	JULE2028.	00115184	221	000a 1955	Star 87 km					-		
2			- BODMINE	10 00 DEC	200 101	00.2	- 000 91 1		-, despective	STANDAD.	-,00013266	-00023594	10027971	00325611	STUTNES.	021 91000	DOMASSN.	Another .	00021483	11081800.	COCOCCO	*1864000"	200.000	-,00300357		- 347304	1000000	THEFT AND	DCD48451	00006121	511 (2884	and a second sec					
5		MODES42	19231040	MODENTE	6165	100001131	260 E 1000	E2E30040	8162000	00011336	22EC 2000	1111000	BUT21040	109999000	00038516	BUTUIDE.	19962000 ·	100000 L	26095080	120019427	T Station	COLOCIDES.	20017557	311551080	HORNZOGD'-	- 0204714	ALL COMP.	interest									
THE O	00034613	01925000.	15090800'-	31.210000	- 1001 AA1100	-, 00019077	11511400	00018213	1000000	- 00010517	.005874NS	100111000	Dictory and	E1481000	00048822	20101030	14121000	1961 1963	BRESCORD	00024428	Contraction -	0111000	- Distant	- 002001	- NEWCORD -	E1650000	TITING .	19612100	A143006-	69620902	-,0003815T	TABABAL .					
-	CDOCKED	Bast 2000		No. 20002.	- 00012800 -	PIELION	195126007	6021100	B1210000'-	- Cluber	00002	000115547	12123000	92421000	011630600	5-29 mg	2 E14402	CHECK & COLOR	01077249	6,752000	STATISTICS.	Dist Close	T221 0000	- 40025x33	-, 00023406	00001) E	Barrows -	04100000	- 10000019	15141200'-	-, 00006130						
		.00000548		-, 00069829-	Constant.		-, 20017665		- DELEGE	D 1000573	10031302	C1070950	1000223001	20012365	20015145	COULTERS.	SHEDGOOD"	00030590	CODE BAT	CREEKE	-, depending	- CODDA NGE	00131577	Manana.	- 1001003	- 0002000	COLORAD .	Annual Susana	CTTRADED.	- DEDWEDSA	-,000016709	1	_			-	
101		0012536W	BEC2300	FICTORIO,	ATATONA.	00055451	-,00002113		17422000	00010442I	COC16865	15410000	17187060	DOM: NO	actitiste	52242000	S100000-			52681360	- MARTINE -	DOUTINES.	00040487	00025540	CHRISTING.	100462		and ball	-, 00056 [54	-, 0001184.92	10012100	and and a second second					
0	1912000	- 00011745		0001114B		DODDAR28	- 00002712	00000383	A110124	21602000	86125900.	Thrank and	261400000	20062325	10024200	SET87800,	DOC 1010		.00071245	15131000"-	101110101		(0009308	W\$21000"	COUNTY IN	WELNESDO" -	- Million and	21121120		CENESO05.	PART (1990)	CREATING.		-	_		-
		2 06	148M0300			- 000 (B. 6)	00011955	SEBICINE.	FI 270 no.	2221 0340	00018166	1955 00	2 in prints	POOT SWEEK	D HIDS IC	12 152 0 10	0 178765	0 0 1206	01050735	LI GPOLD	0 03 85	166 2 0 4 -	Dittersize	- 0 0 0259	0 018 30	- 3 03 150 -	- 000 5111	- 0 0 16319				-		_	-		
	003 4 35	00003015	1651 IQCO	16280000	000 8948	- 0000102	- 1213338	0 008 83	111111	1003320	0039211	1 269 5	STANKUUV	MODR201	CR ISCOL	00.21.25	0.110 mm	0.0744.7	- 0 0 1231	0 DAS+8	15681 U	C.Daßwig	10119710	-,001246 VB	000 59 2	Statistics -	- 0 522kn							ļ			
6		Internation.	57951000	Tanivini -	- MURRAL	.0007103	-, POINTABO	10012546	CENTRA CO.	ADDITION OF		There is a second secon		+.AD122309-	Bomissio	- MALERAN	00000118		OBSTREET	00016613		000000661	- AD 101194			ADDITION -	- 31306431	- DODANGO	CARING -	00049626	CONSTRUCTION OF THE OWNER OWNER OF THE OWNER OWNER OF THE OWNER	Antenna .	-, boxwar	11045908-			-
	SHOT	2422000	10153673	- 00011312	2001544	21000940	.00044290	BELLEN.	00021648		REPARENT	- 400 Ball	T AND DRAW	BUILDER'S	00088272	and the second	ADD DE 155	SAEQUON"	(CD01-00)*	#\$1,50000-	TOTOLOGICA	96236030	-,40029680	HUIMP-	21010101	STREET,	BCBKURDE.	.00005481	Platable .	LUNITION"-							
	_			COCKTOR OF	Suntrike2	18561004°-	0000648	- BESTATA	404021/29	10030151	THE PARTY OF	- 0002100	- 44229262		1963 1994		# LEE2000	#2CLOW*+	- 1120511		2915	0532	.00055370		0292	1191	1221	. 00023391	0.054 151	BALL LINE	POUSADA						-
	ETERON	Ka621902	BUANDOO.	20011200	WARDEN	22361030		CLEANER'	SECECTED -	-,40017943	1021-01430	THE OWNER WATCHING	00005289	00105104	Zisenen.	40011782			40011212	2289450000	ALL DECIDENTS	- 0011031	BACE00007	84443300	BELLEN.	CH10100	ALL LAND	100301100									
			2 2	- 2	2	±:	2	2 5	: ::	ŝ	20	5 8	1 23	24	1	2 2	: 2	29	8	5 6	1 2		ŝ	10	5	R 2	-	Ę	¥				5		2 23	5 5	20

Table 24. Neekly Catchebility Estimates for Age J Adjusted for Abundance

		2111101 -	TANKAR.	1218000 ·	and	PODA L	Castred.	Sticked.	5211009*	2152902	ALENDA-	002229	8202308		1451000-	100000	A LOUGH	0000163	0001000	BC100.	1940000	.0001854	THE PARTY OF			191010	11 K2000"-	1212000	SPECIAL CONTRACTOR	164000						
181		96077000.	48291100	20510009	Constant of	COSCNOW.	DOM NUT	40115754	86618080	PL0001470	BC667884	3660000	000151000	\$1562000	A11281000	ALLINON .	APPENDING A	044020400	11011000.	D0027462	20092000	28(10000)	1 YOR COM	12272000 -	18110000	82215558										
				ATRUATION.	1	000202551	10172464	PRODUCES.		19090001	21111200	1000000	ACCASES.	.00023588	GN631000*	1911100	010022212	Disesso	PINISTR9	36141007	00004345	DECEMPS'-	122/1000	2100000	0075546	ABANDA	CS290000'	*******	PLOCING'-	00149622	. 0020125a	Cherrona .				
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Table 25 Meekly Catchubility Estimates for Aga 4 Adjusted for Abundance

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Table 36. Meskiy Catchability Estimates for Age 5 Adjusted for Abuncance

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feble 27. Keekly Catchability Entimates for Age 6 Adjusted for Abundance



Table 24. Meewiy Catchability Estimaten for Age 7 Adjusted for Abundance





AGE GROUP	CHI-SQUARE	D.F.		Р
0	19.9943	13		.0954
1	53.3286	14	<	.0001
2	36.4897	14		.0009
3	74.6490	14	<	.0001
4	52.5875	14	<	.0001
5	10.2981	8		.2447
6	3.2400	4		.5185

TABLE	30.	Results of	Friedman's Te	st for	Randomized	Blocks
		on Weekly	Catchability	Coeffic	ients.	

TABLE 31. Results of Friedman's Test for Randomized Blocks on Catchability Coefficient Residuals (after adjusting for abundance).

AGE GROUP	CHI-SQUARE	D.F.	P
0	15.1587	5	.0097
1	134.3467	14	< .0001
2	42.9290	14	.0001
3	76.0417	14	< .0001
4	51.0357	14	< .0001
5	9.5059	8	.3014
6	12.6400	4	.0132

AGE	Correlation	<u># Data Points</u>
0	-0.170	200
1	-0.196	560
2	-0.269	551
з	-0.161	468
4	-0.287	356
5	-0.325	195
б	-0.519	39
7	-0.956	5
8	-1.000	2

TABLE 32. Correlation Coefficients Between ln(q) and ln(N).





AGE 0

AGE 1







AGE 2









AGE 4

AGE 5







AGE 6





		21	LIGI	ence		CHC		COL D.						
73	75	79 	77	76	74	80	Age 71	1 78	81	82	69	68 	72	70
71 	69	68	70	78	77	80	Age 76	2 72	81	75	79	73	82	74
70 	69	76	68	79	77	74	Age 80	3 78	75	71	82	81	73	72
70	76	78	80	69	82	77	Age 75	4 74	68	79	71	73	72	81

FIGURE 5. Results of Multiple Comparisons for Age Groups Whose Catchability Coefficients Show Significant Differences Between Years.

alpha = .05

Bars indicate no significant difference was found between years.

Years arranged in ascending order of ranks of catchability coefficients for each PTU.

Bars indicate no significant difference was found between years.

Years arranged in ascending order of ranks of catchability coefficients for each PTU.

VITA

Steven Michael Atran

Born on 25 September 1955 in Quincy, Massachusetts. Graduated from Milton High School, Milton, Massachusetts in 1973. Received a B.S. in Fisheries from the University of Washington in 1977. Field biologist for Ichthyological Associates, Middletown, Delaware, 1978-1979. Entered Master's degree program in College of William and Mary, School of Marine Science in 1981. Employed since 1985 as a computer programmer/analyst at the Sandy Hook Laboratory of the National Marine Fisheries Service, National Oceanic and Atmospheric Administration, in Highlands, New Jersey.