

1986

Fluctuations in the Catchability Coefficient of Atlantic Menhaden, 1968-1982

Steven M. Atran

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<https://dx.doi.org/doi:10.25773/v5-c2z0-bb40>

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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

1986



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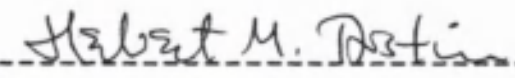


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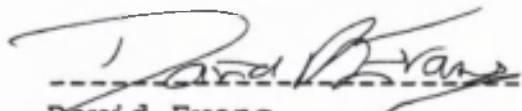
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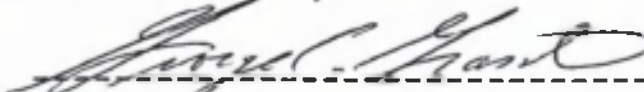
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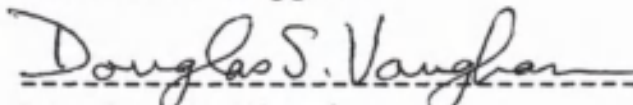
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ACKNOWLEDGMENTS

I am grateful to my committee chairman Dr. Joseph G. Loesch for his patience and support, and for providing me with financial assistance through an assistantship. Thanks are also due to the rest of my thesis committee for their support, patience and suggestions.

I would like to thank Douglas S. Vaughan of the Stock Dynamics Branch, Southeast Fisheries Center, Beaufort Laboratory, for making the Atlantic menhaden catch and effort data available, and for his many helpful comments and suggestions. Thanks are also due to Bob Lukens of the Virginia Institute of Marine Science for showing me how to use the DIALOUT system to communicate with the National Marine Fisheries Service computer in Seattle.

Several of my coworkers at the Sandy Hook Laboratory, Northeast Fisheries Center, provided helpful suggestions and support. I especially thank Stu Wilk for his support and interest in this thesis, and Anthony Pacheco and Kevin Friedland for sharing with me their knowledge of Atlantic menhaden biology and fisheries. I am grateful to Michele Cox for her assistance with graphics, and to Wally Morse for guiding me through SAS/GRAPH.

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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 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
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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 nets. In 1826, the purse seine was invented by John Tallman 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 seines. Coal-fired steamers came into use after the Civil 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 ‰ 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 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 ‰ to hypersaline environments of 60 ‰. 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, Oncorhynchus 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

$q_t =$ 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 - 1976 for 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:

$$(C/f)_t = q_t N_t \quad (1)$$

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:

$$q_t = (C_t/f_t) / ((N_t + N_{t+1})/2) \quad (2)$$

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 unnecessary 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 0 through 6. Ages 7 and 8, as well as some years for ages 0, 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:

$$q = aN^{-b} \quad (3)$$

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

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

where \ln indicates Napierian (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 effort 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 the years in the multiple comparisons bar diagrams (figure 6) showed much change.

A weak 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 overriding 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:

$$F = qf \quad (5)$$

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

$$F = aN^{-b}f \quad (6)$$

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 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 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 0 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 apparent in the plot of average weekly catchability coefficient for age 0 menhaden, which is quite different from the plots of older age groups. 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.

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 variability 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 availability 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.;

$$q = kr \quad (1)$$

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, Penaeus merguensis. Morrissy and Caputi (1981) reported that variation in catchability of freshwater crayfish, marron (Cherax tenuimanus) 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 management 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 (Palohimo 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

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

The catch in interval i is given by

$$C_i = N_i E_i$$

$$E = \frac{F_i (1 - e^{(-t_i F_i + M_i)})}{F_i + M_i} \quad (2)$$

The catch in interval $i+1$ is given by

$$C_{i+1} = N_i e^{(-t_i(F_i + M_i))} E_{i+1} \quad (3)$$

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

$$R_i = \frac{C_{i+1}}{C_i} = \frac{e^{(-t_i(F_i + M_i))} E_{i+1}}{E_i} \quad (4)$$

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

$$R_{i+1} = \frac{C_{i+2}}{C_i} = \frac{e^{(-t_i(F_i + M_i) - t_{i+1}(M_{i+1}))} E_{i+2}}{E_i} \quad (5)$$

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

$$\frac{C_{i+k}}{C_i} = \frac{E_{i+k} e^{-t_i(F_i + M_i) - t_{i+1}(M_{i+1}) - \dots - t_{i+k-1}(M_{i+k-1})}}{E_i} \quad (6)$$

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 $L = i-k$,

equation 6 can be written as

$$\frac{C_{i+1}}{C_{i-k}} = \frac{C_{L+k+1}}{C_L} = \frac{E_{L+k+1} e^{-t_L(F_L + M_L) - t_{L+1}(M_L) - \dots - t_{L+k}(M_{L+k})}}{E_L} \quad (7)$$

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

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

Once the array [E] is known, the array [F] may be found by iteration from the following equation (Tomlinson 1970, eq. 7):¹

$$E_i = \frac{F_i (1 - e^{-t_i(F_i + M_i)})}{F_i + M_i} \quad (9)$$

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

$$E_i e^{t_i(F_i + M_i)} = \frac{C_{i+k} E_{i+k} e^{-t_{i+1}(M_{i+1}) - \dots - t_{i+k-1}(M_{i+k-1})}}{C_{i+k}} \quad (10)$$

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)

$$E_i e^{t_i(F_i + M_i)} = \frac{F_i (e^{t_i(F_i + M_i)} - 1)}{F_i + M_i} \quad (11)$$

Once F is estimated, E can be estimated by

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

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

$$N_i = \frac{C_i}{E_i} \quad \text{where } E \neq 0 \quad (13)$$

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

PTU	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
6	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 and 14 refer to January and February of the following year

Table 7. Abundance Estimates for Age 5

PTOL	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
1									25115876	3386565
2									24388131	6226432
3									22989354	9998248
4									21049509	5019810
5									18713877	8872781
6									16581993	6278162
7	3685074								17957602	8849555
8	3621810								15413539	7735368
9	3551913								14832221	7616177
10	3458514								13351585	6917148
11	3404691								12255778	6289655
12	3383539								11107613	6289655
13	3318787								10275325	5614531
14	3256582								9453095	4998013
15	2936486								8673036	3935848
16	2894436								7951621	3601955
17	2956603								7318087	3601955
18	2831394								6817081	3601955
19	2801174								6433988	3601955
20	1877880								6035051	3601955
21	1749876								5617319	3601955
22	1406198								5181162	3601955
23	1337169								4727319	3601955
24	1253342								4257319	3601955
25	1179848								3777319	3601955
26	1151847								3287319	3601955
27	1105069								2787319	3601955
28	1047211								2277319	3601955
29	1035313								1757319	3601955
30	997045								1237319	3601955
31	976903								717319	3601955
32	904034								203319	3601955
33	899014								133319	3601955
34	865290								63319	3601955
35	857634								33319	3601955
36	850442								33319	3601955
37	843114								33319	3601955
38	835050								33319	3601955
39	807270								33319	3601955
40	602037								33319	3601955
41	596950								33319	3601955
42									33319	3601955
43									33319	3601955
44									33319	3601955
45									33319	3601955
46									33319	3601955
47									33319	3601955
48									33319	3601955
49									33319	3601955
50									33319	3601955
51									33319	3601955
52									33319	3601955
53									33319	3601955

Table B. Abundance Estimated for Age 6

Year	Age 6 Abundance
1958	185266
1959	181816
1960	168576
1961	154884
1962	148884
1963	95543
1964	84788
1965	93921
1966	81747
1967	81043
1968	83262
1969	79521
1970	78966
1971	78286
1972	77811
1973	38952
1974	38008
1975	38257
1976	32458
1977	33187
1978	32881
1979	32588
1980	14852
1981	12788
1982	12878
1983	12581
1984	12452
1985	8207
1986	14852
1987	12788
1988	12878
1989	12581
1990	12452
1991	8207
1992	156679
1993	114809
1994	113820
1995	112839
1996	111847
1997	109523
1998	109471
1999	109000
2000	83842
2001	82322
2002	82147
2003	82256
2004	81670
2005	81138
2006	158328
2007	157971
2008	156582
2009	148288
2010	147184
2011	145842
2012	145842
2013	122923
2014	121878
2015	120827
2016	119786
2017	118746
2018	87628
2019	2512475
2020	2428897
2021	2407669
2022	2234593
2023	2162238
2024	1854391
2025	1824395
2026	188875
2027	173288
2028	177184
2029	89524
2030	88284
2031	78138
2032	182888
2033	152488
2034	150882
2035	150882
2036	672188
2037	2042749
2038	1925129
2039	1426482
2040	1414151
2041	791288
2042	624574
2043	619182
2044	485788
2045	251
2046	847842
2047	778268
2048	788274
2049	757843
2050	758518
2051	748853
2052	727649
2053	791288
2054	624574
2055	619182
2056	485788
2057	251

Table 3. Abundance Estimates for Age 7

PTID	1968	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1														
2														
3														
4														
5														
6														
7	478711													
8	415531													
9	411831													
10	488281													
11	336451													
12	333561													
13	320881													
14														
15														
16														
17														
18														
19														
20														
21														
22														
23														
24														
25														
26														
27														
28														
29														
30														
31														
32														
33														
34														
35														
36														
37														
38														
39														
40														
41														
42														
43														
44														
45														
46														
47														
48														
49														
50														
51														
52														
53														

500000
296270
292355

Table 10. Abundance Estimates for Age 0

Year	Age 0
1970	
1971	
1972	
1973	
1974	
1975	
1976	
1977	
1978	
1979	
1980	
1981	
1982	
1983	
1984	
1985	
1986	
1987	
1988	
1989	
1990	
1991	
1992	
1993	
1994	
1995	
1996	
1997	
1998	
1999	
2000	
2001	
2002	
2003	
2004	
2005	
2006	
2007	
2008	
2009	
2010	
2011	
2012	
2013	
2014	
2015	
2016	
2017	
2018	115200
2019	112000
2020	
2021	
2022	
2023	
2024	
2025	
2026	
2027	
2028	
2029	
2030	
2031	
2032	
2033	
2034	
2035	
2036	
2037	
2038	
2039	
2040	
2041	
2042	
2043	
2044	
2045	
2046	
2047	
2048	
2049	
2050	
2051	
2052	
2053	

TABLE 20. Coefficients Used in the Catchability-Abundance Relationship: $\ln(q) = \ln(a) - b * \ln(N)$

Age	$\ln(a)$	b
0	5814.75146	260.73114
1	13.64552	1.07412
2	-4.78667	0.14681
3	-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 30. Results of Friedman's Test for Randomized Blocks on Weekly Catchability Coefficients.

AGE GROUP	CHI-SQUARE	D.F.	P
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 31. Results of Friedman's Test for Randomized Blocks on Catchability Coefficient Residuals (after adjusting for abundance).

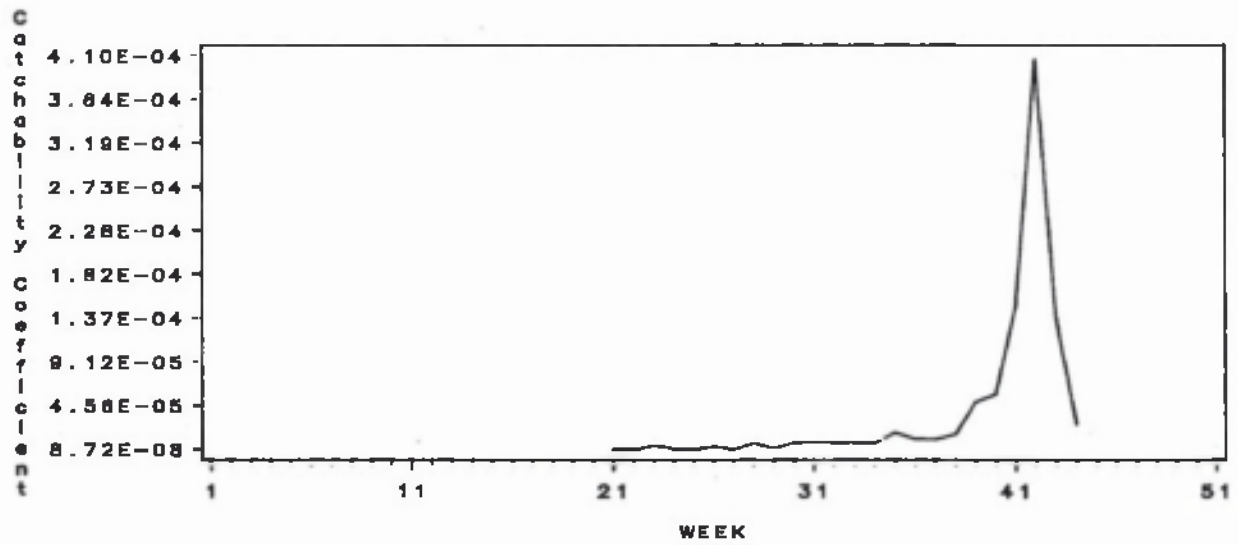
AGE GROUP	CHI-SQUARE	D.F.	P
0	15.1587	5	.0097
1	134.3467	14	< .0001
2	42.9290	14	.0001
3	76.0417	14	< .0001
4	51.0357	14	< .0001
5	9.5059	8	.3014
6	12.6400	4	.0132

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

<u>AGE</u>	<u>Correlation</u>	<u># Data Points</u>
0	-0.170	200
1	-0.196	560
2	-0.269	551
3	-0.161	468
4	-0.287	356
5	-0.325	195
6	-0.519	39
7	-0.956	5
8	-1.000	2

Figure 1. Average weekly catchability coefficient - ages 0 and 1

AGE 0



AGE 1

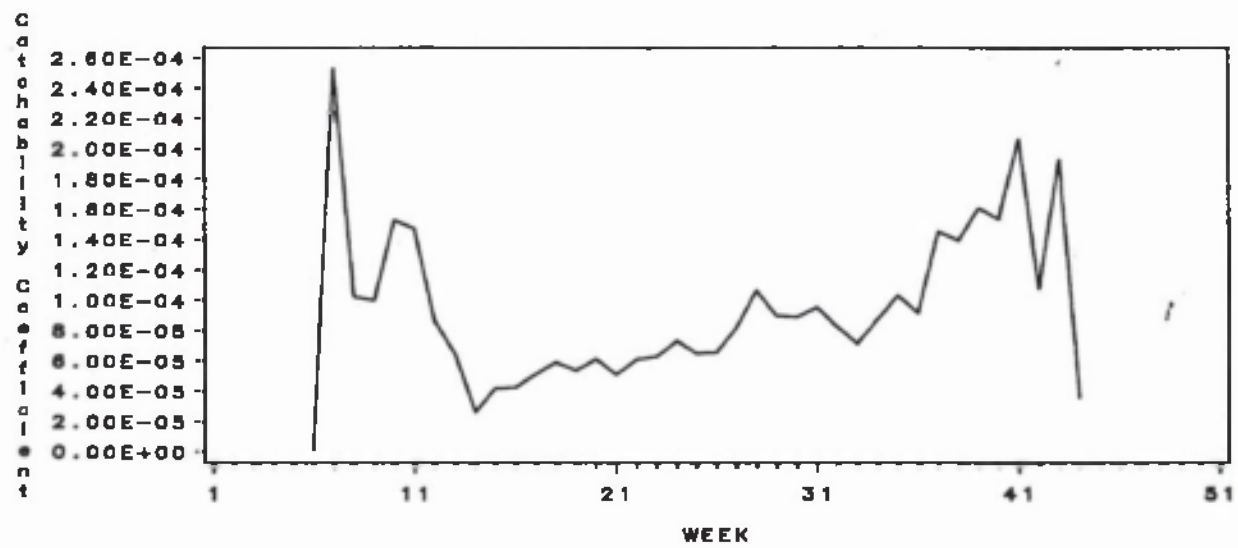
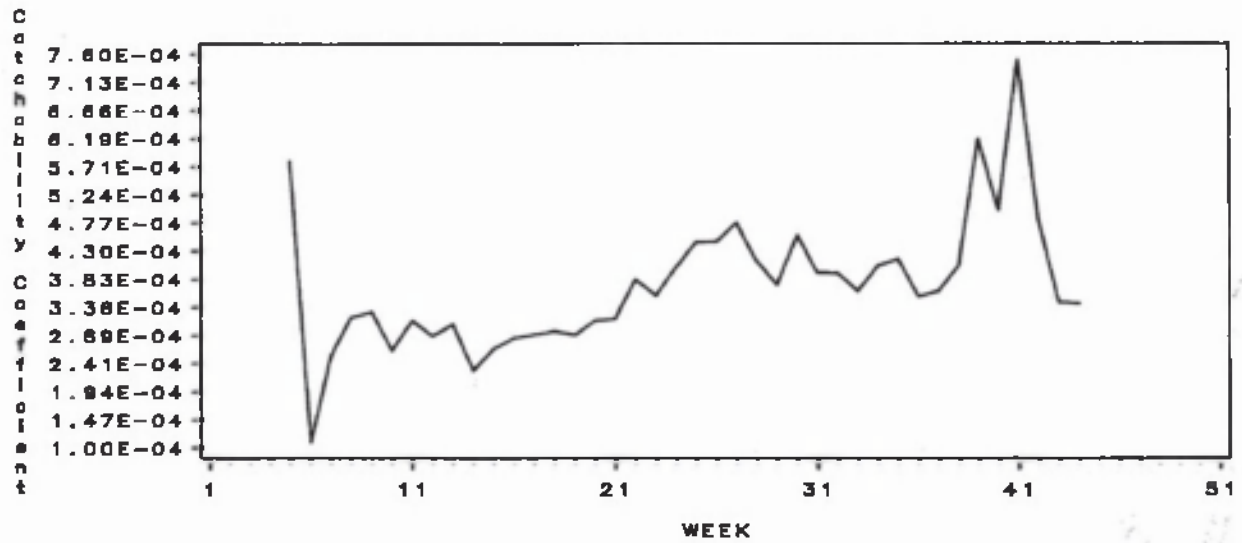


Figure 2. Average weekly catchability coefficient - ages 2 and 3

AGE 2



AGE 3

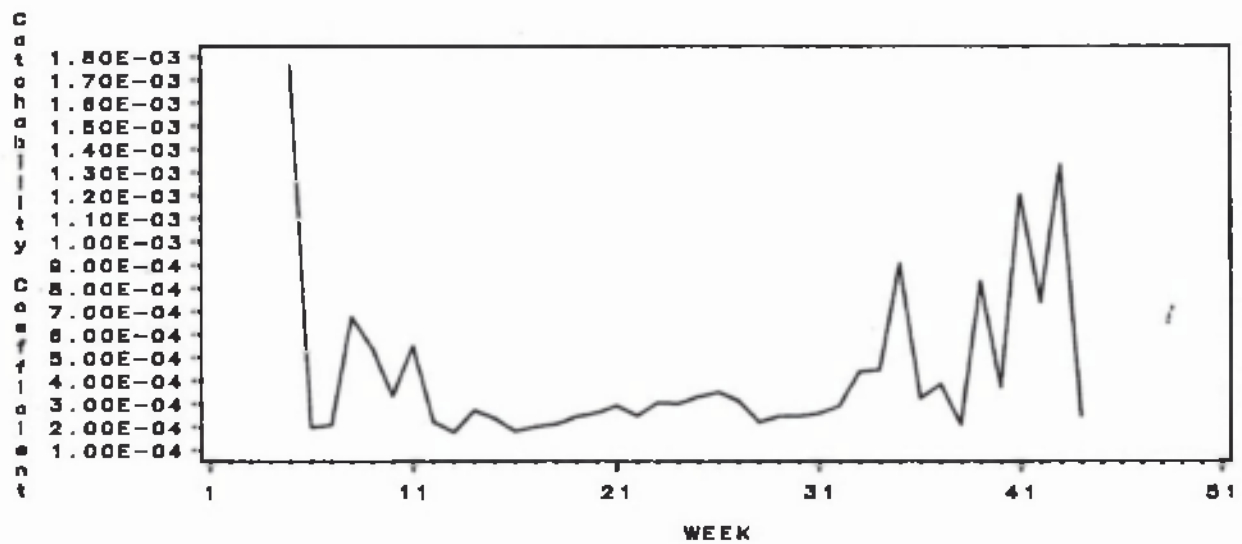
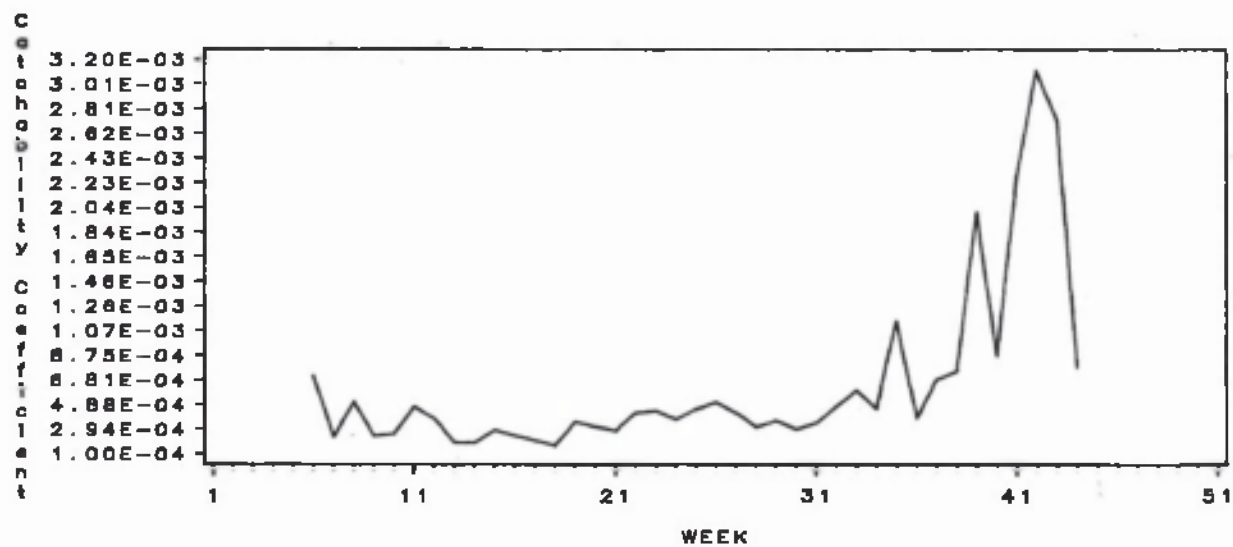


Figure 3. Average weekly catchability coefficient - ages 4 and 5

AGE 4



AGE 5

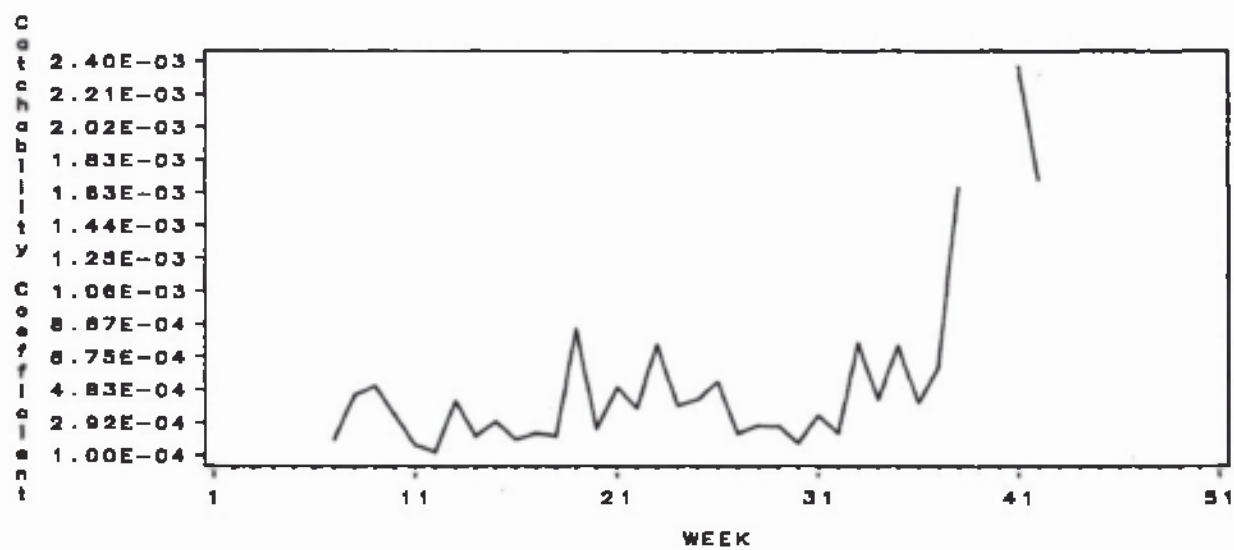
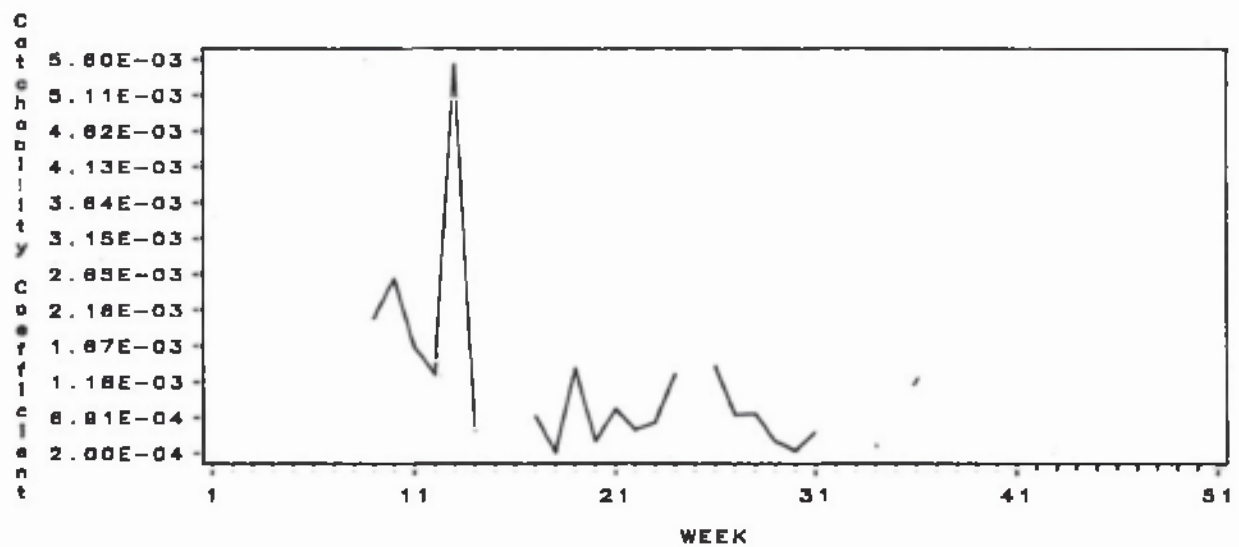


Figure 4. Average weekly catchability coefficient - ages 6 and 7

AGE 6



AGE 7

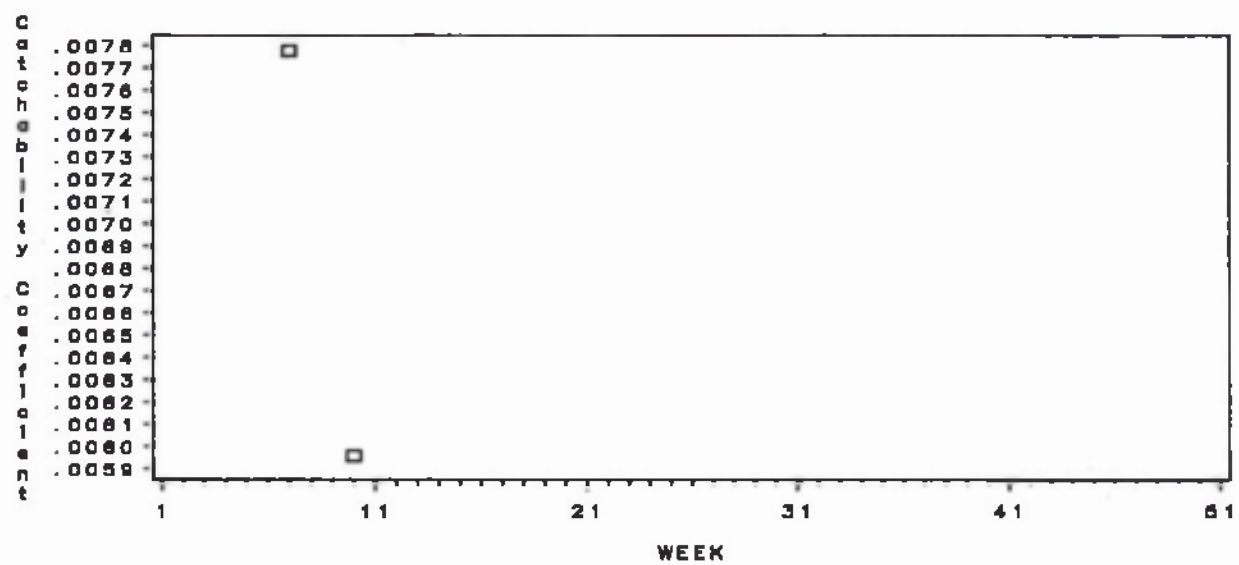
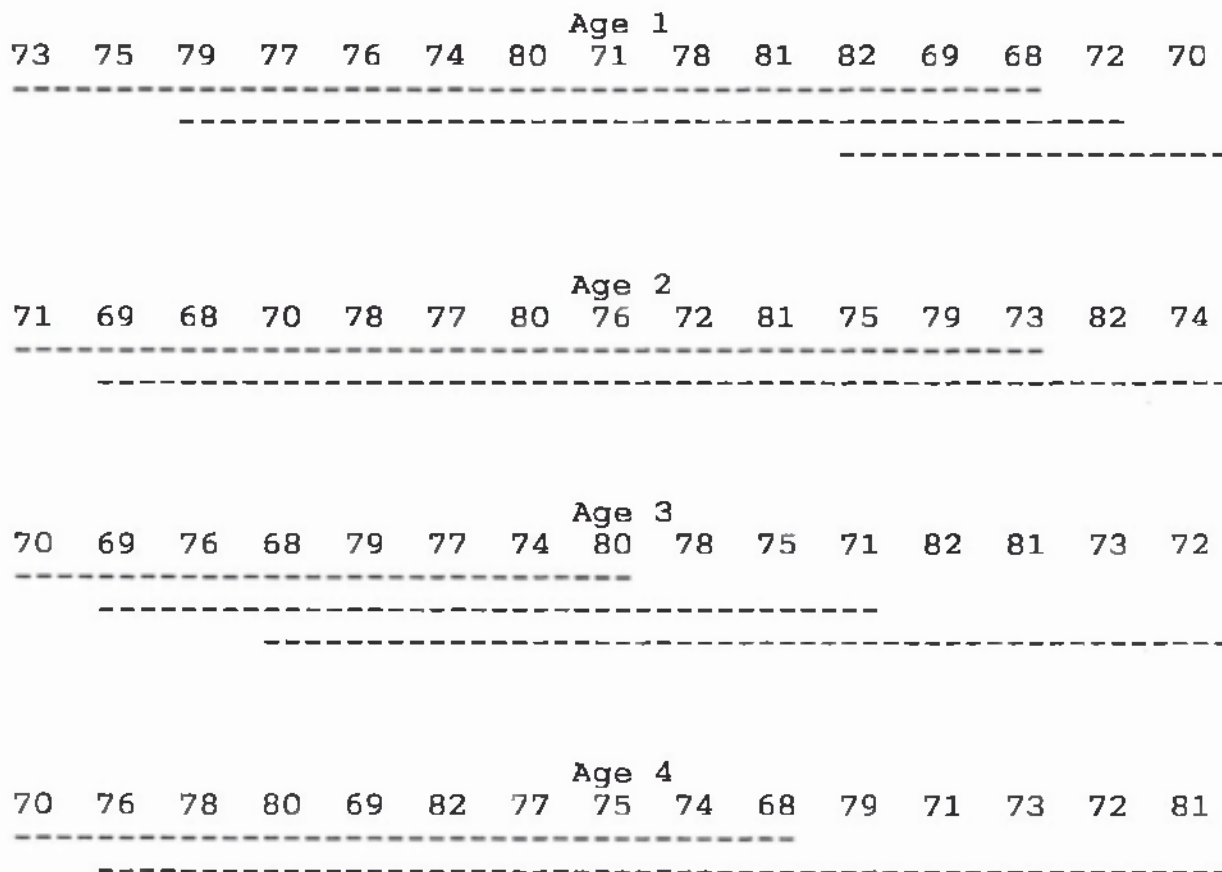


FIGURE 5. Results of Multiple Comparisons for Age Groups Whose Catchability Coefficients Show Significant Differences Between Years.

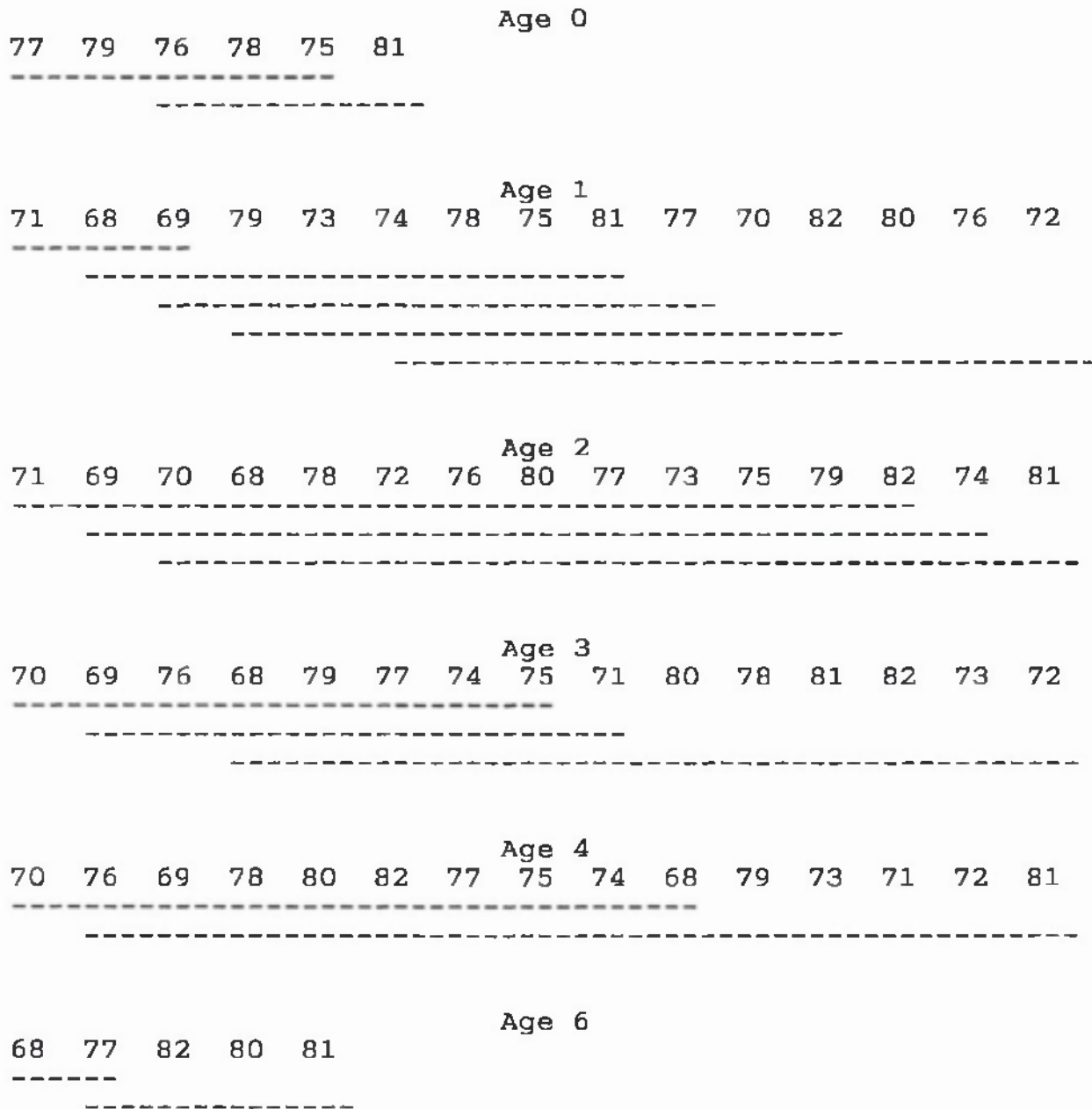


alpha = .05

Bars indicate no significant difference was found between years.

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

FIGURE 6. Results of Multiple Comparisons for Age Groups Whose Catchability Residuals 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.

VITA

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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.