INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Order Number 9115410

Population dynamics of young-of-the-year striped bass, *Morone saxatilis*, populations, based on daily otolith increments

Kline, Lisa Lynn, Ph.D.

The College of William and Mary, 1990

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

POPULATION DYNAMICS OF YOUNG-OF-THE-YEAR STRIPED BASS, MORONE SAXATILIS, POPULATIONS, BASED ON DAILY OTOLITH INCREMENTS

A Dissertation

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

Doctor of Philosophy

by
Lisa L. Kline
1990

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

Doctor of Philosophy

Lisa L. Kline

Approved, December 1990

James A. Colvocoresses, Ph.D.
Committee Co-Chairman/Advisor

Herbert M. Austin, Ph.D.
Committee Co-Chairman/Advisor

Mark E. Chittenden, Jr., Ph.D.

John E. Olney, M.S.

Evon P. Ruzecki, Ph.D.

Louis J. Rugolo, Ph.D.
Maryland Department of Natural Resources
Annapolis, Maryland

TABLE OF CONTENTS

CHAPTER I - Validation of daily increment deposition in otoliths of juvenile striped bass, <u>Morone saxatilis</u>.

CHAPTER II - Factors influencing the production of daily growth increments in otoliths of juvenile striped bass, <u>Morone saxatilis</u>.

CHAPTER III - Population dynamics of juvenile striped bass populations in Virginia river systems.

CHAPTER IV - Limitations of the back-calculation of length-at-age from daily growth increments, and application to juvenile striped bass populations.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my co-committee chairman, Dr. James A. Colvocoresses, for his advice and support during all phases of this project. I also wish to thank my co-committee chairman, Dr. Herbert M. Austin, and the other members of my committee, for their constructive review of this manuscript. The support and guidance provided by Loius Rugolo during the final stages of completion of this manuscript is also gratefully acknowledged.

Many thanks, also, to my fellow students who assisted me in the course of my studies with their critical advice and good humor. In particular, I would like to thank Dean Estes, Donald Seaver, and the other students and summer aides who assisted in the field-collections; Alan Blair and the other personnel at the Harrison Lake Fish Hatchery for their allowing collections to be made in the hatchery ponds; and, the personnel of the Jacksonville National Fish Hatchery for providing samples for the laboratory experiments.

Finally, I would like to thank my family for their support and patience throughout my studies.

LIST OF TABLES

LIST OF FIGURES

Validation of daily increment deposition in otoliths of juvenile striped bass up to 80 days of age was provided through sequential sacrifice of known age hatchery-reared fish in 1987 and 1989, and through tetracycline marking of otoliths of cage-cultured striped bass in 1989. Ages of fish between 80-110 days old were consistently underestimated by 1-3 growth increments.

Known age juvenile striped bass were raised in the laboratory in 1989 under controlled environmental conditions. These experiments provided evidence of an endogenous circadian rhythm controlling daily increment deposition in juvenile striped bass otoliths.

Juvenile striped bass were collected in the 4 Virginia river systems in 1986 and 1987. A total of 542 otoliths were aged using daily growth increments. Comparisons of back-calculated birthdate distributions between populations showed consistency between rivers within years, but not between years. Variations in cohort growth rates appeared to be related to the relative cohort size of fish surviving to the juvenile stage. A comparison of mortality for 14-day cohorts showed no trends between early and late hatched fish, and no relationship was found mortality and average growth rates for these cohorts.

Population growth rates for the period June-September were linearly modelled, and ranged from 0.301-0.597 mm/day and 0.027-0.124 g/day. Mortality estimates for 60-90 day old striped bass ranged from 1.88-3.98% loss/day. Catch-per-unit-effort, as measured as the number of fish per seine haul, ranged from 4.0-29.6. Growth rates in both length and weight were positively correlated with condition factor and stomach fullness, suggesting food availability may play an important role in regulating juvenile striped bass growth. There was no apparent relationship between growth and CPUE. The relationships between growth and mortality, and mortality and CPUE, are ambiguous, and more estimates are needed to determine whether a density-dependent effect is controlling year-class strength and recruitment into the juvenile stage.

POPULATION DYNAMICS OF YOUNG-OF-THE-YEAR STRIPED BASS, *MORONE SAXATILIS*, POPULATIONS, BASED ON DAILY OTOLITH INCREMENTS

GENERAL INTRODUCTION

Striped bass, Morone saxatilis, have historically supported one of the most important commercial and recreational fisheries in the Chesapeake Bay. Due to low levels of production from the mid-1970's to the mid-1980's, regulatory agencies in Maryland and Virginia were forced to institute strong conservation measures on the taking of striped bass in Bay waters to protect residual stocks. The recent history of striped bass abundance has been one of variable reproduction, periodically bolstered by the production of dominant year classes that supported increased landings (Raney 1952). Dominant year classes are characterized by the production of unusually large quantities of recruits in a single year so that the members of this age group dominate the standing stock for a considerable period of time (Merriman 1941). Koo (1970) discussed a distinct pattern of fluctuation in striped bass abundance with an alternation of high and low landings occurring about every six years in Maryland. However, results of autocorrelation analyses and spectral analyses do not support the hypothesis of a simple six-year cycle in the appearance of dominant year classes (Van Winkle et al. 1979). Dominant year classes have occurred approximately every six years beginning in 1934, although the 1952 and 1976 year classes did not follow this apparent trend (ASMFC 1981).

As a long-lived, slow growing, multi-aged species, a strong year class of striped bass can dominate the population for two or more years. Since striped bass enter the Chesapeake Bay fishery as two-year-olds, the onset of high production in landings appears two years after a dominant year class is spawned (Goodyear 1984). For example, in 1974, 1975, and 1976, the dominant 1970 year class comprised 60, 75, and 55% of the total landings in the Chesapeake Bay, respectively; even though many other year classes were present. Once the harvest of the 1970 dominant year class was complete, the total landings for the Atlantic Coast dropped drastically. According to the Maryland young-of-the-year surveys, recruitment of striped bass was below the 1954-74 average between 1975 and 1980 (ASMFC 1981).

Large fluctuations in year classes of striped bass in the Chesapeake Bay have influenced striped bass populations in more northern waters (Boreman and Austin 1985; Koo 1970; Mansueti 1961; and Merriman 1941). Berggren and Lieberman (1978) estimated that the contribution of the Chesapeake Bay stocks to the harvest along the Atlantic coast may have been as high as 90 % when the 1970 dominant year class entered the mixed-stock coastal fisheries. More recently, Van Winkle and Kumar (1982) provided evidence that the relative contribution of the Hudson River stock varies from 5 to 50 % due to variable year class strength in the Chesapeake Bay.

The formation of a striped bass dominant year class appears to be caused by density-independent environmental factors affecting survival of early life stages (Cooper 1981; Kernehan et al. 1981; and Ulanowicz and Polgar 1980). A density-independent population is characterized by an age structure that varies greatly over time; catch-per-unit-effort that varies considerably from year to year; and abundances of immature fish that are not related to parent stocks (Ulanowicz and Polgar 1980). Recent studies by the Maryland Department of Natural Resources (unpublished data) has shown that a marked stock-recruitment relationship exists when density-independent factors are filtered from this relationship. Density-independent factors appear to have most of their effect under conditions of medium-high parent stock size. However, when stock sizes are depressed, favorable environmental conditions will not produce a dominant year class. There appears to be a minimum threshold of stock abundance below which strong reproduction will not occur.

Fay et al. (1983) found that water flow, both velocity and volume, are important to the spawning success in California waters and in the Roanoke River, North Carolina. Higher flows during spawning produced the most successful year classes (Fay et al. 1983). Merriman (1941) found a significant correlation between certain strong year classes on the Atlantic coast and lower than normal yearly temperatures. Koo (1970), however, found no correlation between temperature and year class strength. The general conclusion is that the temperature regime prior to and during spawning and early development is more important than mean yearly temperature (Fay et al. 1983; and Kernehan et al. 1981). Dominant year classes appear to have always been proceeded by a colder than normal winter (Fay et al. 1983), however, a low temperature during late winter and early spring does not necessarily mean a dominant year class will be produced (Merriman 1941).

Recent research has shown that events during the early life history of many fish species are important in determining population dynamics, species interactions, and community structure of the adult stage (Rice et al. 1987). Mechanisms controlling recruitment in the first year of life include both abiotic and biotic factors, such as competition and food availability. There is evidence that fluctuations in abundance of many fish populations are often caused by variable survival rates during early life history stages due to the interactions of these factors (Fritz et al. 1990; and Crecco and Savoy 1985). Year class strength of striped bass appears to be relatively set by the time the juvenile stage is reached; therefore, survival and growth data in the early life stages of this species may provide insights into mechanisms of recruitment and factors influencing year class strength.

Time of striped bass spawning is dependent on water temperature, with peak spawning occurring at 14-15oC (Morgan et al. 1981; and Austin 1980). Dey (1981) found that temperature fluctuations in the Hudson River estuary in 1976 contributed to the production of more than one period of peak spawning. Since earlier hatched striped bass have a longer period for feeding and growth in their first year (Chuganova 1959), first winter survival is increased (Dey 1981). Rate of growth during the first growing season may affect survival rate, rate of maturation, and the time of appearance on the spawning grounds (Krebs 1978; Carlander 1974; Kramer and Smith 1960; and Chuganova 1959). Tiller (1943) suggested that striped bass that were small as yearlings showed a greater increase in growth rates in their second year of life, however, complete growth compensation did not occur. Variations in growth rates will affect year class size and the availability of legal size striped bass to the fishery (Austin and Hickey 1978).

Current knowledge of growth rates of young-of-the-year striped bass is based on length-frequency analysis (Trent 1962; Mansueti 1961; Robinson 1960; Mansueti 1958; Vladykov and Wallace 1952; Merriman 1941; and Scofield 1931), the direct measurement of change in length or weight over time (Dey 1981), or through limited mark-recapture studies (Koo and

Ritchie 1973). The discovery of daily growth increments on otoliths of many fish species (Pannella 1971) has enable age determination of larval and juvenile fishes (Williams and Bedford 1974) and provided a valuable tool to facilitate studies of growth, survival, and recruitment mechanisms during early life history stages. Research efforts in the 1970's focused mainly on validation of daily increment deposition (Barkman and Bengston 1987; Geffen 1986; Campana and Neilson 1985; Laurs et al. 1985; Campana 1984B; Radtke and Dean 1982; Brothers et al. 1976; Struhsaker and Uchiyama 1976). As suggested by Campana and Neilson (1985), validation on a species-specific basis is the first essential step in all daily increment studies, and must be performed for the entire early life history stage under study. Daily increment deposition has been validated for larval striped bass up to an age of 50-60 days (Houde et al. 1990; Secor and Dean 1989; and Jones and Brothers 1987). More recent research has focused on applications of the daily increment aging technique to studies of growth, survival, and recruitment processes (Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989; Deegan and Thompson 1987; Savoy and Crecco 1987; Essig and Cole 1986; Crecco and Savoy 1985; Jones 1986; Penney and Evans 1985; Miller and Storck 1984; Methot 1983; Victor 1982; Methot 1981; Townsend and Graham 1981).

Enumeration of daily increments in early life stage otoliths provides the ability to determine the age of individual fish, back-calculate hatching dates, and calculate growth rates and survival estimates during this critical developmental period. Increment width data is used to back-calculate individual growth histories, provided a relationship is found between somatic growth and growth of the otolith. Recent studies on South Carolina juvenile striped bass by Secor and Dean (1989) provide evidence that slower growing fish may have larger otoliths, resulting in inconsistent otolith-fish size relationships. They suggested that proportionality between somatic and otolith growth should be verified on each individual population under study before application of the back-calculation procedure. Neilson and Geen (1982) suggested that otolith studies provide a means of assessing environmental conditions that affect growth and survival in early life history stages. The integration of a long-term database of growth and mortality on a population- or cohort-specific basis with time series changes in biotic and abiotic factors (temperature, salinity, river flow, and food availability) may lead to a better understanding of the mechanisms controlling recruitment and year class strength of striped bass.

There has been much controversy concerning the factors that either cause or influence the production of daily growth increments. The most popular current theory is that daily increment deposition is under the control of an endogenous circadian rhythm (Mugiya 1987, 1974; Campana and Neilson 1985;

Rosa and Re 1985; Townsend and Shaw 1982; and Tanaka et al. 1981). An endogenous rhythm is caused by a pacemaker in the organism itself with cyclic environmental factors acting as synchronizing agents or 'Zeitgeber' (Aschoff et al. 1982). Endogenous rhythms are frequently correlated with environmental cycles although they are not necessarily a direct response to them. Campana and Neilson (1985) were the first to formulate a hypothesis that links daily increment deposition to an endocrine-driven endogenous circadian rhythm. The hypothesis predicts that one increment should be deposited per day at regulate intervals due to the circadian rhythm. Temperature and feeding cycles not having a 24-hr periodicity would then from increments in addition to the one already deposited. When Pannella (1971) first described daily growth increments in fish otoliths, he stated that the causative factors of the daily cycle were unknown, but that there may be some relation to known circadian rhythms in the behavior, metabolism, and physiology of fishes. This theory is currently the most popular theory among current workers in this field of study, however the literature provides a plethora of controversial data, some supportive of the theory of an endogenous rhythm (Mugiya 1987; Campana and Neilson 1985; and Rosa and Re 1985) and others supporting a stronger influence of environmental factors, such as temperature (Marshall and Parker 1982; Pannella 1980; Brothers er al.

1976; and Irie 1960), and feeding cycles (Neilson and Geen 1982; Pannella 1980; Taubert and Coble 1977; and Liew 1974).

STUDY DESCRIPTION AND OBJECTIVES

The purpose of this study was three-fold: 1) to provide evidence of daily deposition of otolith growth increments in juvenile striped bass, 2) to determine factors influencing the production of daily increments in otoliths of juvenile striped bass, and 3) to apply the otolith aging technique to wild populations of young-of-the-year striped bass in Virginia river systems so as to provide population- and cohort-specific estimates of growth and mortality.

Since juvenile striped bass collected from field sampling between June-September are known to be older than 50 days of age it was necessary to perform a validation study to confirm daily increment deposition for this life history stage (Chapter I). Validation was performed through the sequential sacrifice of known-age hatchery-reared striped bass and through tetracycline marking of striped bass held in field enclosures under ambient environmental conditions.

In order to determine the influence of an endogenous circadian rhythm on daily increment deposition in juvenile striped bass, known age striped bass were raised in controlled temperature and photoperiod environments. Daily otolith increments were enumerated to determine if daily increment deposition continued under constant environmental conditions.

The relationship between average growth rate and mean increment width was also examined, to determine the reliability of using increment width measurements to estimate growth rates of individual fish.

This study applied the otolith aging technique to wild striped bass populations in three Virginia river systems to evaluate growth and mortality. The interrelationships between growth, mortality, abundance and average condition factor, which is an indication of the well-being of a fish population, may provide insights into mechanisms of recruitment and the influence of density-dependent factors on juvenile striped bass populations. Furthermore, the calculation of birthdate distributions can lead to cohort-specific estimates of growth and mortality (Methot 1983; Crecco and Savoy 1985). The back-calculation of length-at-age was critically evaluated for young-of-the-year striped bass due to the recent evidence of an uncoupling between somatic and otolith growth in several fish species (Secor et al. 1989; Mosegaard et al. 1989; and Reznick et al. 1988). An evaluation of the otolith-fish size relationships of juvenile striped bass was made on a population-specific basis and an effort was made to determine the cause of any variability in these relationships. Average length-at-age and growth rate-at-age were calculated for the populations showing a good fit between otolith and somatic growth, so as to evaluate growth of the population during the entire early life history.

Chapter I - Validation of daily increment deposition in otoliths of juvenile striped bass, *Morone saxatilis*.

INTRODUCTION

Since Pannella (1971) first described the existence of daily growth increments on fish otoliths, the application of increments to fish age and growth determination has been applied to a variety of teleost species (see reviews by Jones 1986; and Campana and Neilson 1985). The majority of these studies have shown that environmental factors may influence the deposition of calcium carbonate on a daily basis, thereby interfering with the daily growth record of the otolith. Marshall and Parker (1982) and Taubert and Coble (1977) found that deposition was non-daily at extremely low temperatures in Onchorynchus nerka, and Lepomis and Tilapia species, respectively. Jones and Brothers (1987) showed that deposition was less than one increment per day in starved fish, while Neilson and Geen (1982) found evidence of more than one increment per day when fish were fed four times daily. Photoperiod has also been linked to daily deposition of increments by Mugiya (1987), Radtke and Dean (1982), and Taubert and Coble (1977). Geffen (1982) reported that deposition was directly related to somatic growth rate and that daily deposition occurs only above a critical growth rate. Campana and Neilson (1985) suggested that the erroneous interpretation of subdaily increments, or the lack of resolution of light microscopy below 1 um, may have caused a deviation the actual number of increments in several of these studies.

Even though the majority of published results to date provide very good evidence that daily increment deposition may be a universal phenomenon shared by most teleost species, validation of daily increment deposition is a critical prerequisite to the application of otolith microstructure ages to growth and mortality studies (Campana and Neilson 1985). Ideally, validation of daily deposition should closely mimic natural conditions, and be performed for the entire early life history stage under study. Campana and Neilson (1985) and Gjosaeter et al. (1984) concluded that the two best approaches for the purpose of validation involve: 1) the sequential sacrifice of known age fish held in large pond enclosures; or 2) the examination of fish previously marked with tetracycline and held under ambient field conditions.

Antibiotics of the tetracycline series are incorporated into areas of growing calcified tissues usually within a day of application, due to the formation of complexes with calcium of growing bone tissue (Hettler 1984; Campana and Neilson 1982; Wild and Foreman 1980; and Weber and Ridgway 1967). Chemical marking techniques usually employ oxytetracycline hydrochloride either through injection (Campana 1983; Campana and Neilson 1982; and Wild and Foreman 1980), immersion

(Hettler 1984; and Neilson and Geen 1984), or dietary intake (Weber and Ridgway 1967). The width of the tetracycline mark depends on the duration of administration and the rate of bone formation, while the intensity of the mark is dependent on tetracycline dosage. Observation of the deposited tetracycline is accomplished by illumination under ultraviolet light (Campana and Neilson 1985; Hettler 1984; and Weber and Ridgway 1967).

The validation of daily increment deposition was pursued using a two-fold study approach. First, known age hatchery-reared young-of-the year striped bass were sequentially sacrificed, and secondly, a cage-culture experiment of tetracycline marked striped bass was performed. In both phases of this investigation, a comparison of light microscopy and scanning electron microscopy was performed.

MATERIALS AND METHODS

Juvenile striped bass were obtained from the Harrison Lake Fish Hatchery, Virginia in 1987 and 1989. Fish in 1987 were hatched from Chesapeake and Delaware Canal brood stock on May 2, while fish in 1989 were hatched on May 2 from Mattaponi River brood stock. At approximately 30 days of age fish were stocked into hatchery ponds, where they were raised under similar environmental conditions and feeding regimes. Juvenile striped bass were collected from the same pond on a monthly basis in 1987 and bi-monthly in 1989.

Standard, fork, and total lengths were measured and wet weight was taken before otolith removal. In 1987, all three pairs of otoliths were removed to determine which was best suited to age determination. Asteriscus and lapilli were ground in the sagittal plane after attachment to a microscope slide with Crystalbond, a thermosetting resin. Sagitta were removed and stored dry in 96-well tissue culture trays. Sagitta were later mounted in flat embedding molds using liquid spurr following the procedure of Haake et al. (1982). The hardened blocks of Spurr were cut transversely with a Beuhler low-speed isomet saw and were attached to a microscope slide with Crystalbond. The block was ground against 600 and

400 grit wet-dry sandpaper until the primordium was reached. The otolith was flipped and ground from the other side until there was no superposition of growth increments. Polishing was performed on a piece of Microcloth containing 0.3 micron alumina polishing compound.

Each otolith was read on two separate occasions at 400-600X magnification under an Olympus compound microscope connected to the BIOSONICS Optical Pattern Recognition System (OPRS). If the percent difference between readings was less than 10 per cent, the mean of the readings was accepted; however, if the difference between readings was greater than 10 per cent, the readings were discarded. The left and right otoliths were removed from 27 striped bass and otolith growth increments were enumerated to determine if counts differed between otoliths. Readings were verified through scanning electron microscopy (SEM) analysis. Otoliths were prepared for SEM by etching with 5 per cent EDTA (pH=8) for 13-16 minutes. Three increments were added to the mean increment count to adjust for the delay in first increment deposition (Jones and Brothers 1987). Least-squares linear regression equations of known age versus mean increment count were calculated for all data in each year and for truncated data sets.

Validation of daily increment deposition was also performed by tetracycline marking of otoliths of juvenile striped bass collected by seine in 1989 and then held in cages in the Pamunkey River. Tetracycline marking was performed by immersion of 25 juvenile striped bass (approximately 40-60 mm standard length) in a NaCl water bath containing 300 ug/mL oxytetracycline (OTC) for 3 days. At concentrations less than 300 ug/mL tetracycline it was impossible to observe the tetracycline mark after sectioning of the otolith and at higher concentrations 100% mortality occurred. After tetracycline marking, fish were placed in a cylindrical cage constructed of PVC tubing and polyethylene mesh (2' deep, 2' diameter), which was then attached to a pier at river mile 50. All surviving fish were sacrificed after 28 days, and otolith increments after the OTC mark were counted under ultraviolet light.

To determine if a relationship exists between daily increment deposition rate and growth rate, growth and deposition rate estimates were obtained from the 1987 and 1989 Harrison Lake Fish Hatchery data and from the constant light and constant dark laboratory experiments (Chapter II). Growth rate estimates were obtained from the slope of the regression of standard length on estimated age, while increment deposition rate was determined from the slope of the regression of mean increment count on known age. A slope significantly different from zero indicates a possible relationship between somatic growth and deposition of daily increments.

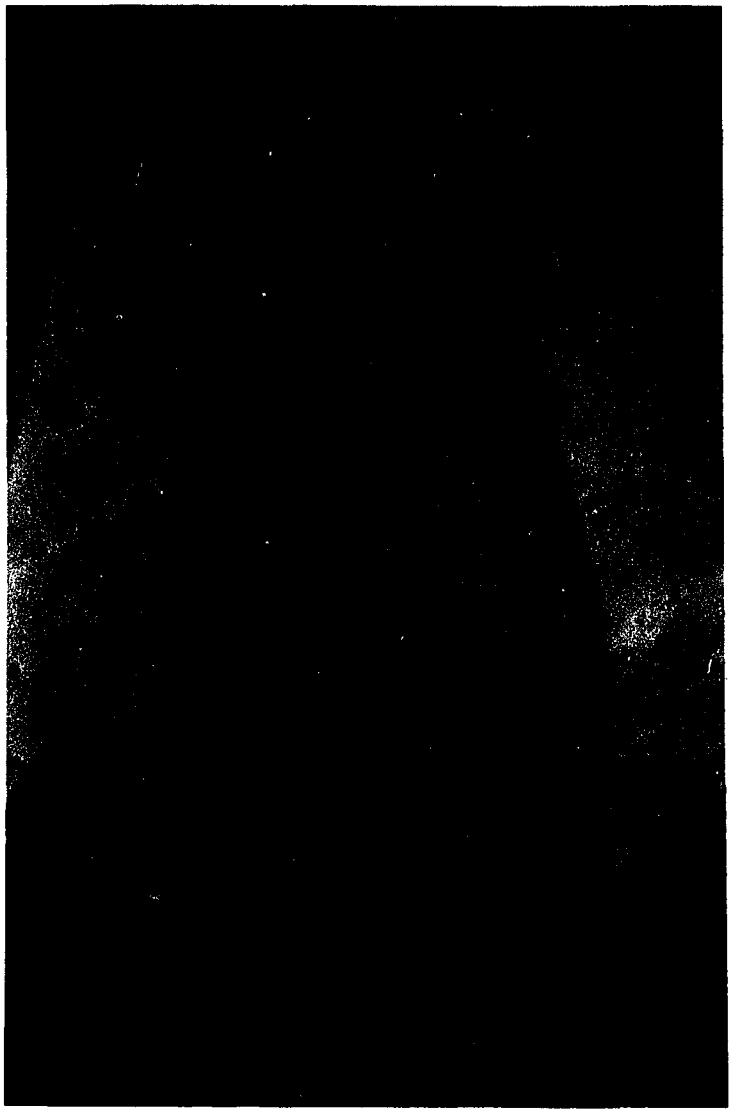
RESULTS

OTOLITH STRUCTURE

Preliminary analysis of 10 hatchery-reared juveniles to determine which otolith was best suited to aging revealed that the asteriscus showed no daily increments. Both the lapillus and the sagitta required grinding and polishing; however, due to the concavo-convex shape of the otoliths, the sagittal section did not elucidate all increments from the primordium to the edge of the otolith. Distinct increments could be discerned near the primordium and margin of the otolith, however, the otolith thickens between these areas, making it impossible to define a sagittal transect on which all increments can be discerned.

Because growth increments could not be uniformly defined in the sagittal section, all sagittal otoliths were processed in the transverse section with daily growth increments enumerated along the long axis of the resulting section (Figure 1.1). Since increments were distorted along some portions of this axis, counts were made along line segments laid out in a zigzag manner around these areas while maintaining as near a straight transect as possible. A growth increment is defined as a bipartite structure, consisting of

Figure 1.1. Photograph of transverse section of sagittal otolith showing daily growth increments (400X magnification).



an incremental and a discontinuous zone (Mugiya et al 1981). When viewed under light microscopy, the incremental zone appears as a translucent band, while the discontinuous zone appears opaque.

One to four subdaily increments were discerned within the first thirty days of growth under light microscopy. Subdaily increments were not as prominent as daily increments and were made to disappear by focusing on the surface of the otolith. Due to the thickness of the otolith section (approx. 10 um), it may be possible that the subdaily increments are an artifact of attempting to focus through the otolith.

One of the 40 otoliths analyzed was composed of both aragonite crystals and a more translucent material, which was presumably vaterite. Five of the 40 otoliths (12.5%) had two primordia within the nucleus. The primordia were approximately 2-3 um apart, with the first increment surrounding both primordia, thereby causing no difficulty with enumeration of growth increments. Vateritic otoliths and otoliths containing two primordia were also observed in otoliths of striped bass collected in the field (Chapter III).

HATCHERY VALIDATION

A paired t-test on mean increment counts from the left and right otoliths of 27 juvenile striped bass showed no significant difference (P=0.613). Therefore, no distinction was made between left and right otoliths for the purpose of this study.

A total of 35 otoliths were processed in 1987, however only 28 otoliths (80%) met the criterion for inclusion in the analysis based on the less than 10 per cent difference between paired readings. Ages of fish older than 156 days were less reliable than younger fish, as seen from the increase in the standard deviation and range of the September and October samples (Table 1.1). In 1989, 22 of 28 otoliths (78.6%) were included in the analysis. All standard deviations and ranges were lower in 1989 (Table 1.2), which may have been due to better preparation techniques and enumeration skills acquired through practice.

Least-squares linear regression equations of known age versus mean increment count were calculated for all data in each year, as well as for the pooled data sets (Table 1.3). Coefficients of determination for all regressions ranged between 0.98-0.99, indicating a high linear relationship between known age and mean increment count. Significance tests rejected the null hypothesis that the slope was equal to one for all regressions. Significance tests for an intercept equal to zero were significantly different when all data was included in the analysis, only partially significant when data was truncated to the end of August in 1989 and the end of September in 1987, and non-significant when data was truncated to mid-July. These differences appear to reflect

Table 1.1. Descriptive statistics of growth increment count data for hatchery-reared juvenile striped bass collected monthly from 15 July-15 October in 1987.

COLLECTION DATE	N	KNOWN AGE	MEAN	STD	RANGE
07 JULY	10	74	73.0	3.56	68.3 - 79.0
19 AUGUST	6	118	111.2	3.97	104.0 - 115.3
25 SEPTEMBER	6	156	144.5	6.04	137.0 - 154.3
25 OCTOBER	6	175	155.0	5.29	149.5 - 164.5

Table 1.2. Descriptive statistics of growth increment count data for hatchery-reared juvenile striped bass collected bi-monthly from 21 June-26 September in 1989.

COLLECTION DATE	N	KNOWN AGE	MEAN	STD	RANGE
21 JUNE	5	44	43.7	0.57	43.0 - 44.5
06 JULY	2	59	57.5	0.71	57.0 - 58.0
18 JULY	3	71	69.0	1.32	68.0 - 70.5
02 AUGUST	3	86	82.7	2.31	80.0 - 84.0
15 AUGUST	3	99	93.7	0.76	93.0 - 94.5
30 AUGUST	3	114	109.3	0.58	90.0 - 110.0
13 SEPT	0	---	-----	----	---------
26 SEPT	3	141	133.0	0.89	131.0 - 135.0

Table 1.3. Least-squares linear regression equations of mean increment count versus known age, and tests of significance, for 1987, 1989, and pooled data for hatchery-reared juvenile striped bass. Equations are for all data in each year, as well as for truncated data sets.

YEAR	DATE	N	EQUATION	R-SQ	P(SLOPE=1)	P(INT=0)
1987	JULY-OCT	28	Y= 11.7+0.83X	0.98	0.0001**	0.005**
	JULY-SEPT	22	Y= 7.98+0.87X	0.98	0.0002**	0.0199*
1989	21JUNE-26SEPT	22	Y= 2.99+0.93X	0.99	0.0001**	0.0009**
	21JUNE-30AUG	19	Y= 2.81+0.93X	0.99	0.0001**	0.0041*
	21JUNE-18JULY	10	Y= 2.50+0.94X	0.99	0.0188*	0.0779NS
POOLED DATA	JUNE-OCT	50	Y= 8.40+0.86X	0.99	0.0001**	0.0001**
	JUNE-SEPT	44	Y= 5.48+0.09X	0.99	0.0001**	0.0007**
	JUNE-AUG	35	Y= 4.49+0.91X	0.99	0.0001**	0.0104*
	JUNE-JULY	23	Y= 2.70+0.94X	0.95	0.2352NS	0.4222NS

the non-linearity of the data after mid-July. An ANCOVA analysis to compare the known age versus mean increment count regressions from July to September in 1987 and June to September in 1989 showed no significant differences between years (P=0.871).

All tests for a slope equal to one and an intercept equal to zero for the pooled data were significantly different, except for data truncated from June 21 to July 31 (Table 1.3). The decrease in the slope to less than one for data after July 31 may be due to the limited resolution of the light microscope to discern increments less than 1 um in width or due to a cessation of daily increment deposition.

A total of 13 sagitta were analyzed with scanning electron microscopy to determine if resolution was limited with the light microscope (Table 1.4). Scanning electron and light microscopy counts were significantly different (paired t-test, -6.13, P<0.0001), with increment counts from the SEM being significantly lower than counts made on the light microscope. Of the otoliths analyzed using SEM, only 2 had a known age greater than 77 days. Deletion of these two data points from the analysis still showed a significant difference between the techniques, with SEM again showing lower counts (paired t-test, -8.94, P<0.0005). The otoliths of juvenile striped bass are convoluted and constant refocusing is required to enumerate all increments under light microscopy. Use of SEM does not allow the reader to view all increments

Table 1.4. Comparison of mean otolith increment counts made using a light microscope and a scanning electron microscope for known-age hatchery striped bass.

KNOWN AGE	MEAN LIGHT COUNT	MEAN SEM COUNT
68	70.0	62
68	65.5	62
74	74.0	64
74	74.0	60
75	71.0	61
75	68.5	56
77	62.0	67
77	73.0	56
77	68.3	59
77	68.0	56
77	71.0	64
118	107.5	95
118	104.5	89

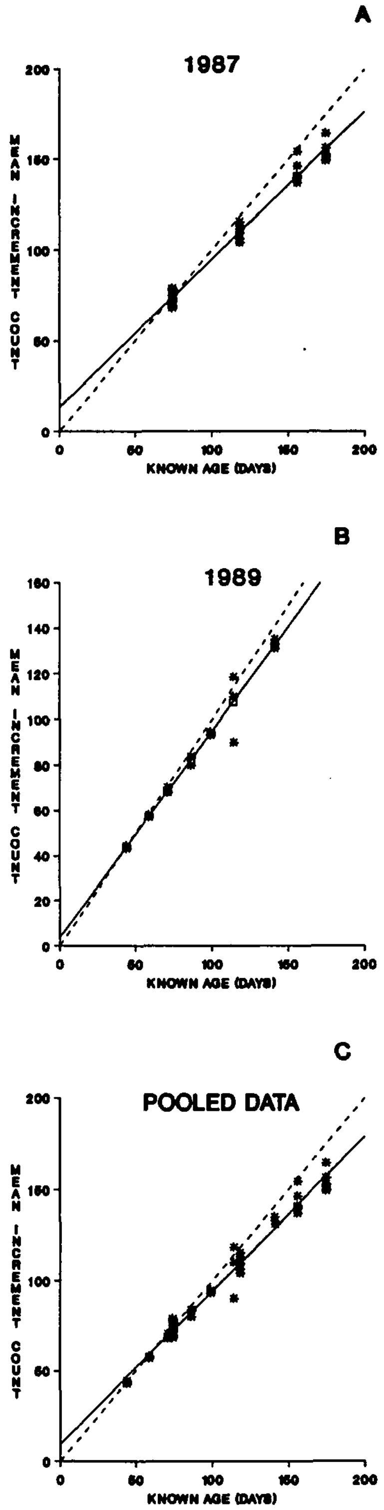
in the flat section due to the convolutions inherent in these otoliths, thereby underestimating increment counts. Further, SEM analysis does confirm the existence of subdaily increments in the first 30 days of growth in striped bass otoliths.

A 1:1 regression line was overlaid with the calculated linear regression lines for the light microscope readings for the 1987, 1989, and pooled data (Figure 1.2). The appearance of an overestimate of ages from 0 to 80 days for the pooled data is caused by the underestimate of ages after 80 days, as can be seen by observing the match between the observed data points and the 1:1 data points up to 80 days of age. A correction factor was calculated for ages greater then 80 days from the difference between the regression lines. This correction factor is applied in later studies on growth and mortality of field collected juvenile striped bass. One increment was added to the age of fish 81-88 days old, two increments to fish 89-100 days old, and three increments to fish aged 101-110 days. Field-collected juvenile striped bass older than 110 days of age were not included in the analyses of growth and mortality (Chapter III). The correction factors applied to ranges of ages for wild fish correspond to a maximum error of 1.2%, 2.2%, and 3.0% respectively.

HATCHERY GROWTH RATE ESTIMATES

Growth rates in length (mm) and weight (g) were calculated from mean length and weight differences between the

Figure 1.2. Known age versus mean increment count for pooled 1987 and 1989 hatchery data showing original data points, the plotted regression line, and a 1:1 regression line.


A
1987
MEAN INCREMENT COUNT
0
50
100
150
200
KNOWN AGE (DAYS)
B
1989
MEAN INCREMENT COUNT
0
20
40
60
80
100
120
140
160
KNOWN AGE (DAYS)
C
POOLED DATA
MEAN INCREMENT COUNT
KNOWN AGE (DAYS)

July 6 (N=10) and September 25 (N=6) samples in 1987, and from the June 21 (N=5) and September 26 (N=3) samples in 1989. Growth rates for the season were 0.682 mm/day and 0.301 g/day in 1987 and 0.703 mm/day and 0.247 g/day in 1989 (Table 1.5). Population growth rates were then calculated as the slope of the least-squares linear regression of standard length and weight on estimated age after application of the correction factor to adjust for the underestimation of ages of the older fish. Regression growth rate estimates were 0.743 mm/day and 0.435 g/day in 1987 and 0.862 mm/day and 0.275 mm/day in 1989 (Table 1.5). Modelled growth rates much higher for growth in weight in 1987, and for growth in length in 1989.

TETRACYCLINE VALIDATION

It was determined through preliminary studies that a concentration of 300 ug/mL of oxytetracycline hydrochloride applied for 3 days was required to mark juvenile striped bass otoliths for examination by this study. The rather extended length of time possibly due to the stress of catch and handling, as well method of thin sectioning of the otoliths for age determination. Eleven striped bass were placed in the cage-culture on August 7, however, only seven fish survived to September 4 at which time the experiment was terminated due to decreasing temperatures. The low survival rate of caged fish may have ben due to the catch/handling stress, stress of the tetracycline marking, and possible holding stress.

Table 1.5. Growth rates in mm/day and g/day for hatchery-reared juvenile striped bass collected in 1987 and 1989. Observed growth rates were calculated from mean length and weight differences between fish sacrificed on 7 July and 25 September in 1987, and from 21 June and 26 September in 1989. Regression growth rates were calculated as the slope of the regression of standard length or weight on estimated age from the otolith aging technique.

	MM/DAY		G/DAY	
YEAR	OBSERVED	REGRESSION	OBSERVED	REGRESSION
1987	0.682	0.743	0.301	0.435
1989	0.703	0.862	0.247	0.275

All otoliths of the seven surviving fish showed a distinct tetracycline mark covering approximately 2 increments. Increments were counted from the innermost OTC marked increment to the edge of the otolith. Counts ranged from 25-27 increments, with a mean of 26.4 and a standard error of 0.283 (Table 1.6). Results of a T-test analysis showed a significant difference between the mean number of increments after the OTC mark and the number of day after tetracycline marking (T=5.81, P=0.0011). The results showed an underestimation of approximately 2 days (range=0-3.3 days), which is consistent with the requisite increment correction factor of 2-3 days as determined from the hatchery data for fish 89-110 days old. Assuming the striped bass used in the cage-culture were hatched in late April-early May, the fish would have been approximately 90-120 day old at sacrifice.

GROWTH RATE VERSUS DEPOSITION RATE

Growth rates ranged from 0.389 mm/day in the dark tank to 0.862 mm/day in the Harrison Lake Fish Hatchery in 1989, while daily increment deposition rate ranged from 0.81 increments/day in the dark tank to 0.93 increments/day in the 1989 Harrison Lake Fish Hatchery data (Table 1.7). The coefficient of determination for the growth rate-deposition rate regression was 0.537, however, the relationship was not significantly different from zero (F=2.31, P=0.267),

Table 1.6. Results of a t-test analysis on 7 cage-cultured juvenile striped bass marked with tetracycline and sacrificed after 28 days.

NO. DAYS AFTER IMMERSION	MEAN COUNT	STD	RANGE	PAIRED T-TEST RESULTS			
				MEAN	STD	T	P
28	26.4	0.748	25-27	-1.64	0.283	-5.81	0.0011***

Table 1.7. Growth rates in mm/day calculated as the slope of the regression of standard length on estimated age for the 1987 and 1989 hatchery-reared fish and for fish raised under constant environmental conditions in the laboratory in 1989 (see Chapter II). Deposition rates (increments/day) for each data set were calculated as the slope of the regression of mean increment count versus known age.

YEAR	LOCATION	MM/DAY	DEPOSITION RATE
1987	HATCHERY	0.831	0.87
1987	HATCHERY	0.862	0.93
1989	LABORATORY (LIGHT TANK)	0.434	0.90
1989	LABORATORY (DARK TANK)	0.389	0.81

indicating no relationship between somatic growth of juvenile striped bass and deposition of daily increments.

DISCUSSION

The microstructure of juvenile striped bass otoliths observed in this study is consistent with descriptions for other teleost species in that they consist of an aragonite crystal structure alternating with a protein matrix to cause daily growth increments (Mugiya et al. 1981; Tanaka et al. 1981; Brothers 1984; Campana 1984; Mugiya 1974; and Degens et al. 1969). The appearance of vateritic otoliths has been documented by Brothers (1984), Campana (1983), and Taubert and Coble (1977). These authors, as well as the present study, observed a cessation of daily increment deposition in vateritic otoliths. Further research is needed to elucidate the reasons for deposition of vaterite on the otoliths of these species. Radtke (1978) observed aberrant sagitta in hatchery-reared larval striped bass, but validated daily deposition of growth increments for 5 days after hatch even though two primordia were present. Since the first growth increment surrounded both primordia in the present study, it was felt that increment counts on these aberrant otoliths were reliable.

Due to differential deposition of calcium carbonate along the lateral and dorsal axes of juvenile striped bass otoliths and the consequent concavo-convex shape of these otoliths, sectioning through the primordium was required. Although Jones and Brothers (1987) found an underestimation of ages of striped bass older than 60 days of age, they did not document the section of the sagitta used in their analysis. The present study showed an underestimation of ages of striped bass greater than 80 days old. It was impossible to determine the cause of this underestimation, however, several explanations are possible: 1) the present techniques of grinding and enumeration are inappropriate for aging older fish, 2) the otoliths of older fish may contain more narrow increments, which are below the resolution limits of light microscopy, and 3) increment deposition may cease to be daily after a certain age or life history stage has been reached.

The appearance of subdaily increments has been observed for a variety of different species (Rice et al. 1987; Tsukamoto and Kajihara 1987; Rosa and Re 1985; Brothers et al. 1983; Campana 1983; Campana and Neilson 1982; Brothers 1981; and Taubert and Coble 1977). It has been suggested that subdaily increments may be an artifact caused by focusing through the thickness of the otolith, however, verification of subdaily increments has been provided in the majority of these studies through scanning electron microscopy. The presence of subdaily increments may cause unreliable ages if they are interpreted as daily increments. In the present study, subdaily increments were confirmed through SEM, and it was relatively easy to identify and isolate subdaily increments through focusing on the surface of the otolith. Several authors have found subdaily increment production under controlled laboratory conditions to be a result of minor temperature cycling (Rosa and Re 1985; and Brothers 1981), and of more than one feeding per day (Rosa and Re 1985; and Campana 1983). Campana (1983) suggested that the presence of subdaily increments may be the result of extremely high metabolic rates of the fish.

Daily increment deposition was confirmed for juvenile striped bass up to 80 days of age through sequential sacrifice of known age fish. After 80 days, there was a slight underestimation of ages, corresponding to less than 3% error for fish between 80 and 110 days old. Results of the tetracycline experiment were consistent with these results and imply either a consistent underestimation of ages of older fish, possibly due to resolution limits of light microscopy, or the non-daily deposition of increments after a certain age.

The underestimation errors from SEM analysis were extremely large for all age groups, thereby providing no evidence of resolution limitations with light microscopy. Jones and Brothers (1987) found an underestimation of 10-20 increments on otoliths of older striped bass, which corresponded to an error of approximately 10-20%. The underestimation of age by Jones and Brothers (1987) is much larger than in the present study and may have been caused by lack of readability of growth increments in the section used. Marshall and Parker (1982) and Taubert and Coble (1977) found cessation of daily increment deposition in sockeye salmon and green sunfish due to a decrease in water temperature below 4 C and 10 C, respectively. Jones and Brothers (1987) and Neilson and Geen (1982) found non-daily deposition in larval striped bass and chinook salmon caused by periods of starvation or excess feeding, respectively. Tsukamoto and Kajihara (1987) provide a very good review of other possible causes of underestimation of ages of older fish.

In the present study, it was impossible to determine the exact cause of the underestimation of ages of striped bass greater than 80 days old. The possibility exists that a decrease in water temperatures in early fall causes either cessation of daily deposition of growth increments for a short period of time or increment widths less than the resolving power of the light microscope. The consistency of the underestimation errors between the two years of hatchery-reared fish and the tetracycline experiment provides corroborating evidence that the application of a 1-3 day correction factor to ages of 80-110 day old striped bass is acceptable.

Average growth rate estimates calculated from the regression of standard length on known age were 0.831 and 0.862 mm/day for the 1987 and 1989 data, respectively, for fish between 44 and 175 days of age. Secor et al. (1989), also using the otolith aging technique, calculated growth rates of 1.0 mm/day in the 1986 and 1.1 mm/day in the 1987 Santee-Cooper, South Carolina striped bass populations, with collections extending from June to July. Trent (1962), using length-frequency analysis, observed growth rates from 0.272-0.433 mm/day in Albemarle Sound, North Carolina striped bass, with collections between June and September. Rathjen and Miller (1957) calculated an average growth rate of 0.45 mm/day for Hudson River striped bass between June and October. Dey (1981) reported higher growth rates for young-of-the-year striped bass in the Hudson River at 0.8 mm/day from mid-June to mid-August. Growth rate estimates for wild striped bass populations in Virginia rivers in 1986 and 1987 ranged from 0.301-0.597 for the period July-August (Chapter III). The variations in growth rates observed among these studies are due partially to the variable time periods for which the growth rates were calculated. The faster growth rates observed for the hatchery-reared fish may also be due to ad libitum feeding in the ponds and the lack of competition for food items. It is also possible that the smaller, slower growing fish also may have been removed from the population through cannibalism.

Geffen (1982) suggested that variations in growth rates of Atlantic herring and turbot control the production of daily growth increments, and during slow growth periods daily deposition does not occur in these species. Juvenile striped bass raised under hatchery and laboratory conditions provided a means to test this hypothesis for striped bass. Growth rates ranged from 0.389 and 0.862 mm/day and were not related to daily deposition of growth increments, however, the lowest deposition rate was observed at the slowest growth rate. It may be possible that at growth rates less than 0.39 mm/day, daily deposition may cease. Further research into this possibility needs to be performed before Geffen's (1982) hypothesis can be fully evaluated.

Validation of daily growth increments in striped bass less than 50 days old has been provided by Secor and Dean (1989) for pond-reared striped bass and by Jones and Brothers (1987) for intermittently starved laboratory-reared striped bass. The present study provides evidence that juvenile striped bass can be accurately aged up to approximately 100 days of age. The sight error involved in aging striped bass between 80 and 110 days is within acceptable limits of the otolith aging technique. This underestimation appears to be fairly consistent for all data collected in this study, however, the exact cause could not be determined. It was felt that a correction factor derived from known age fish applied to ages of older fish would be more reliable than incorporating a consistent bias into growth and mortality estimates.

Chapter II - Factors influencing the production of daily growth increments in otoliths of juvenile striped bass, *Morone saxatilis*.

INTRODUCTION

The purpose of this study was to determine if an endogenous circadian rhythm controlled the deposition of daily growth increments in otoliths of juvenile striped bass. Laboratory experiments were performed under constant temperature and photoperiod regimes using known age striped bass. The relationship between somatic and otolith growth was also examined through otolith radius-fish size and otolith radius-age relationships.

There is much debate concerning the factors which either cause or influence the production of daily otolith increments. The most popular current theory is that daily increment deposition is under the control of an endogenous circadian rhythm. An endogenous rhythm is caused by a pacemaker in the organism itself with cyclic environmental factors acting only as synchronizing agents, as opposed to an exogenous rhythm where the environment is the only cause of the rhythm (Aschoff et al. 1982). Endogenous rhythms are frequently correlated with environmental cycles, although their importance is usually limited to entraining the rhythm to a 24-hr periodicity by response to cyclic signals from the environment (Cloudsley-Thompson 1961; and Aschoff et al. 1982). Under natural conditions there are probably several synchronizing agents maintaining the rhythm at the same time (Cloudsley-Thompson 1961).

One of the generalizations about circadian rhythms is that there is a limited range near 24-hrs within which the period of an endogenous rhythm can be influenced by an external cycle. If a synchronizing agent has a period outside this range of entrainment, the rhythm will not be coupled with the agent and will free-run (Schwassman 1971). An endogenous rhythm in the free-run phase will have a periodicity very close to 24-hr, but have rarely been found to be exactly 24-hours. Evidence for the existence of an endogenous circadian rhythm can be provided by excluding all possible synchronizing agents. Under constant conditions the endogenous rhythm should enter the free-run phase and maintain a periodicity near 24-hr (Bunning 1973; and Hinde 1970). The most convincing evidence for an endogenous rhythm under constant conditions is a periodicity which deviates slightly from 24-hr in constant increments from day to day until a new periodicity, usually slightly less than 24-hr, is reached (Hinde 1970).

For most organisms the light-dark cycle is the most influential synchronizing agent, keeping the endogenous rhythm entrained to a 24-hr periodicity (Schwassman 1971; Bunning 1973; Brady 1979; Bennett 1974; and Hinde 1970). However, it has been claimed that a schedule of feeding once per day can also act as an agent (Aschoff et al. 1982). It has been found that in most cases the endogenous period is only slightly dependent on temperature. Entrainment by temperature cycles can occur, however, it is much less effective than the light-dark cycle (Bennett 1974). Schwassman (1971) suggested that poikilotherms are more easily entrained by temperature cycles than homeotherms.

Bunning (1973), Hinde (1970), and other workers have further shown that many metabolic processes exhibit 24-hr circadian rhythms. Mugiya (1984) has shown that calcium deposition on the otoliths of rainbow trout is controlled by a 24-hr circadian rhythm that is most likely under endocrinological control. Recently, Mugiya (1987) simultaneously measured calcium and protein matrix deposition on a single otolith by monitoring calcium and glutamic acid levels over time. He found that both calcium and glutamic acid varied diurnally and were out of phase, with the most active deposition of otolith matrix occurring during the first half of the nighttime period when calcium deposition was at its lowest level.

Campana and Neilson (1985) have formulated a hypothesis that links daily increment deposition to an endocrine-driven, endogenous circadian rhythm. Tanaka et al. (1981) provided support for this theory by demonstrating that a phase-shifted photoperiod caused a phase-shift in the time of daily increment deposition. They also provided evidence that the cues to formation of the incremental and discontinuous zones were lights-on and lights-off. When the light-dark cycles were suddenly reversed, it took at least 6 days for the rhythm of daily deposition to become adapted to the new photoperiod. Since the pattern of deposition was not affected by a change in lengths of the light and dark phases, it appears that the stimulus of lights-on entrains the rhythm.

The endogenous circadian rhythm hypothesis predicts that one daily increment should be deposited per day at regular intervals due to the circadian rhythm. Temperature and feeding cycles not having a 24-hr periodicity could then form subdaily increments in addition to the daily increment already deposited (Campana and Neilson 1985). This hypothesis is difficult to prove in the laboratory since the period of drift from 24 hours predicted in the free-run phase of the rhythm is inseparable from observational errors when enumerating daily increments on otoliths of certain species.

Evidence for an endogenous rhythm controlling the deposition of daily increments on fish otoliths is further substantiated by the presence of daily increments in deep sea and Arctic fish, in the absence of any environmental factors with a 24-hr periodicity. Rannou and Thiriot-Quievreux (1975) showed that a deep sea species of the genus Coryphaenoides inhabiting an environment with no light has an otolith structure similar to fish in shallow water. Townsend and Shaw (1982) found daily deposition in otoliths of blue whiting from above the Arctic Circle, Evidence for daily deposition was based on age-length data, where there is constant light from May to August and constant darkness from November to February. Therefore, if daily deposition were controlled by photoperiod cycles, daily deposition would only be expected in the autumn and spring, and ages of fish would be underestimated. Townsend and Shaw (1982) suggest that an initial light-dark stimulus was probably not responsible for entrainment early in the life of blue whiting, since hatching most likely occurs in late May or early June during constant light. These researchers feel that while daily cycles in light intensity may be responsible for entrainment, intensity levels could not drop to a threshold low enough to simulate nighttime conditions.

MATERIALS AND METHODS

Approximately 100 striped bass, hatched on April 19 at the National Fish Hatchery in Jacksonville, Florida, were shipped to the Virginia Institute of Marine Science on May 19, when the fish were 32 days old. Ten fish were immediately sacrificed and otoliths were removed and processed to verify daily deposition of increments. The remaining fish were separated equally into two 125-gallon aquaria and allowed to acclimate under natural photoperiod for two weeks.

The aquaria were connected to a cooling system so as to regulate temperature at 21 C to allow for maximum growth of striped bass. Each aquaria was insulated and completely enclosed in black-out plastic. A four foot area around both tanks was also enclosed to guarantee that the experiments would not be affected by natural photoperiods. Water changes were conducted every 7-10 days and salinity was maintained at 2-3 ppt. Water quality tests for ammonia, nitrite, and nitrate ions, as well as pH, were performed every day from May 19 to June 2 and approximately every two weeks thereafter. Temperature was measured at random periods 2-3 times daily throughout the experiment.

Fish in the first tank were raised under constant fluorescent light conditions (30 uEs/m2/s), while fish in the second tank were raised in constant darkness. Fish were fed ad libitum with Purina trout chow at 5-10% body weight, which was approximately 3.75-7.50 g of food/day. The regulation of temperature, a random feeding schedule, and constant photoperiod provided an environment not influenced by periodic cycling of the major factors known to effect daily increment deposition.

Five fish in each tank were sacrificed every two weeks beginning on June 23 and ending on September 2. Standard, fork, and total lengths were measured, and wet weight was taken before removal of the sagitta. Sagitta were processed as previously described (Chapter I). Sample sizes of fish used in the analyses were less than the number of individuals sacrificed due to difficulties in locating the primordium during processing.

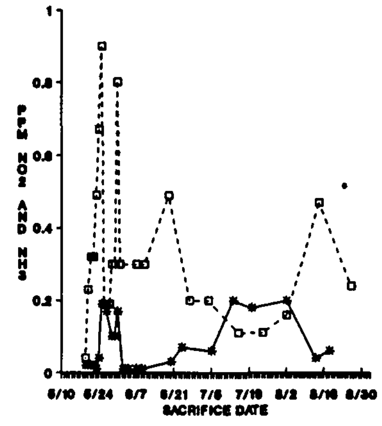
RESULTS

WATER QUALITY

No significant difference was found between ammonia, nitrate, and nitrite levels in the light and dark tanks (t-test, P=0.743), therefore, data was pooled for both tanks (Figure 2.1 A-C). Acceptable water quality levels for survival of any fish species raised in aquaria are less than 0.2 ppm ammonia, less than 0.1 ppm nitrite, and less than 20 ppm nitrate. Ammonia and nitrate levels were within the acceptable range throughout the experiment (Figures 2.1 A and B). Nitrite ions peaked to 1.0 ppm on May 18, but reached the acceptable level of less than 0.1 ppm by May 30. Increases to slightly higher levels (approximately 0.5 ppm) were observed on June 20 and August 15 (Figure 2.1 A). These increases in nitrite ions after the start of the experiment on May 19 did not appear to have a significant effect on the results of these experiments. pH levels ranged from 6.5-7.0 throughout the experiment, which is within the acceptable range for juvenile striped bass survival. Daily temperatures ranged from 18.0 to 23.0 C, and showed no diurnal cycling throughout the experiment. Mean daily temperatures reached 22.0 C by early June and remained within the range of 20.5-

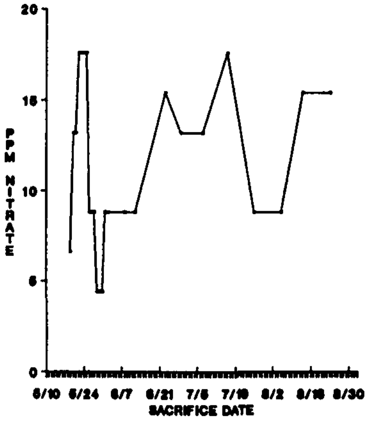
Figure 2.1. Results of water quality tests for laboratory experiments under constant environmental conditions. A: Ammonia (-x-x-x-) and nitrite (-□-□-) levels, B: Nitrate ion levels, and C: Mean tank temperatures. Data was pooled for the light and dark tanks.

A



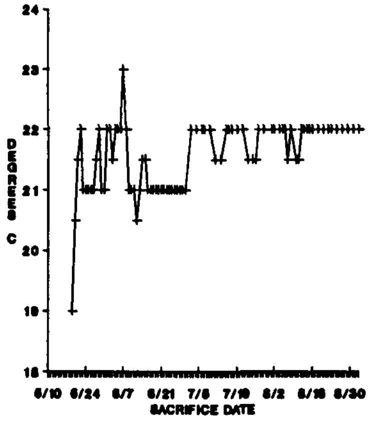
1
0.8
0.6
0.4
0.2
0
PPM NO2 AND NH3
5/10
5/24
6/7
6/21
7/5
7/19
8/2
8/16
8/30
SACRIFICE DATE

B



20
15
10
5
0
PPM NITRATE
5/10
5/24
6/7
6/21
7/5
7/19
8/2
8/16
8/30
SACRIFICE DATE

C



24
23
22
21
20
19
18
DEGREES C
5/10
5/24
6/7
6/21
7/5
7/19
8/2
8/16
8/30
SACRIFICE DATE

23.0 C, with no obvious cycling in mean daily temperatures occurring from May 19 through September 2 (Figure 2.1 C).

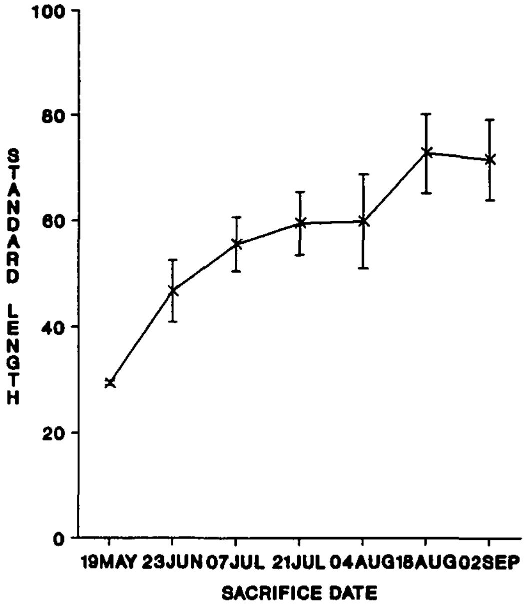
FISH AND OTOLITH GROWTH

The mean length of sacrificed fish was 29.4 mm standard length on May 19 and 46.6 mm on June 23 in both the light and dark tanks (Figure 2.2 A and B). Growth in length as indicated by sacrificed fish remained relatively constant from June 23 to August 4 in the light tank, with lengths ranging from 55.5-55.9 mm during this period (Figure 2.2 A). Mean length of sacrificed fish increased to 72.7 mm by August 18, and then decreased to 71.6 mm by September 2. The apparent decrease in mean length is probably an artifact of the small subsample of fish sacrificed on each sampling date (5 fish). The increase in standard deviation about the mean length with time indicates that growth becomes highly variable between individuals with time and that later subsamples are becoming less reliable as being completely representative of somatic growth within the tank. Growth in length in the dark tank increased at a slower rate, with standard length increasing from 47.4 mm on July 7 to 60.0 mm by September 2, and again showed an increase in variability about the mean length with time (Figure 2.2 B).

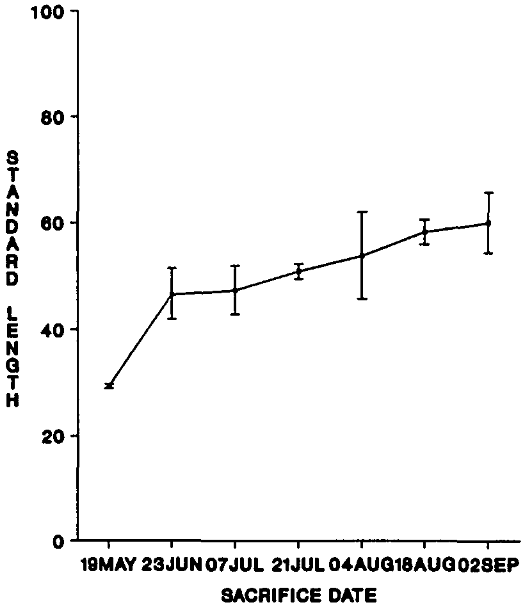
Growth in weight in both the light and dark tank showed similar trends to growth in length, with the sacrificed fish exhibiting the greatest weight on August 18 in both tanks

Figure 2.2. Mean standard length (mm) +/- 1 STD of sacrificed fish by sacrifice date. A: Fish raised under constant light conditions, B: Fish raised under constant dark condtions.

A


100
80
60
40
20
0
STANDARD LENGTH
19MAY
23JUN
07JUL
21JUL
04AUG
18AUG
02SEP
SACRIFICE DATE

B


100
80
60
40
20
0
STANDARD LENGTH
19MAY
23JUN
07JUL
21JUL
04AUG
18AUG
02SEP
SACRIFICE DATE

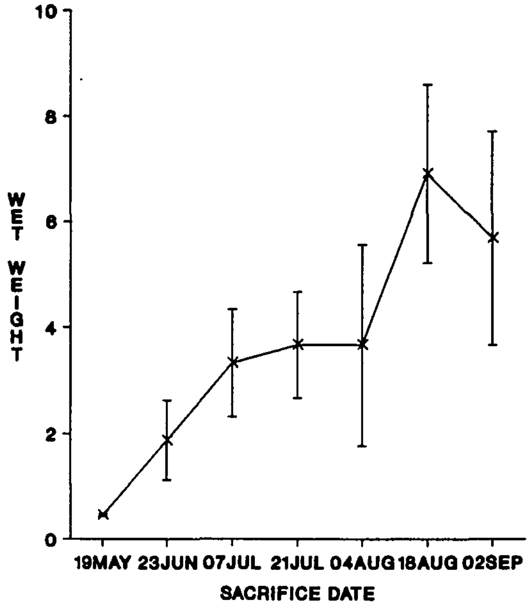
(Figures 2.3 A and B). Mean weight of the sacrificed fish decreased from 6.91 g on August 4 to 5.69 g on September 2 in the light tank, and from 3.40 g to 3.29 g in the dark tank during the same period, indicating some sampling bias towards larger fish in the 18 August sample or towards smaller fish in the 4 August and 2 September samples. Growth rates in length and weight for the period from May 19 through September 2 were 0.406 mm/day and 0.050 g/day in the light tank and 0.294 mm/day and 0.027 g/day in the dark tank.

Otolith growth appeared to parallel fish growth in both length and weight in both tanks (Figure 2.4 A and B). In the light tank, otolith growth was rapid from May 19 through July 7 when fish growth was gradually increasing. Apparent fish growth slowed from July 7 to August 4, while mean otolith size declined. Both fish and otolith mean size increased from August 4 to August 18 and decreased on September 2. In the dark tank, both fish and otolith size appeared to gradually increase throughout the experiment, while growth remained relatively constant.

The relationship between fish and otolith growth was further examined by plotting standard length of each individual fish against the respective otolith radius (Figure 2.5). This plot shows a linear relationship between somatic growth of juvenile striped bass and growth of the otolith, with otolith growth increasing with an increase in standard length. One fish sacrificed on August 4 from the dark tank

Figure 2.3. Mean weight (g) +/- 1 STD of sacrificed fish by sacrifice date. A: Fish raised under constant light conditions, B: Fish raised under constant dark condtions.

A


10
8
6
4
2
0
WET WEIGHT
19MAY 23JUN 07JUL 21JUL 04AUG 18AUG 02SEP
SACRIFICE DATE

B

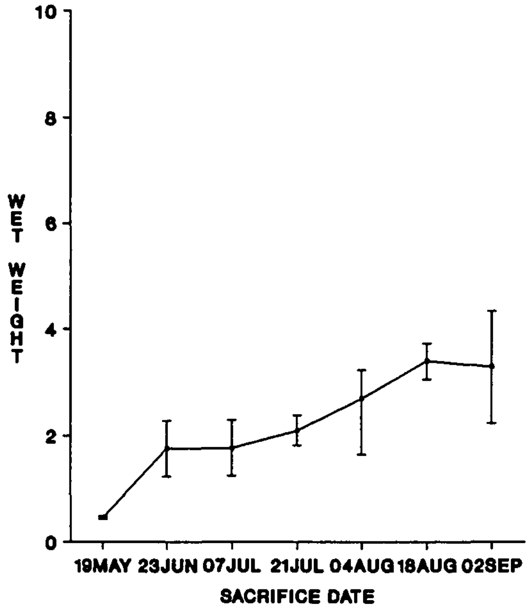
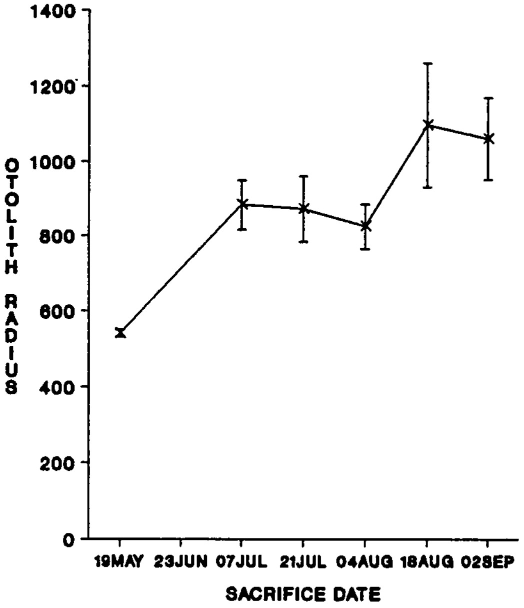

10
8
6
4
2
0
WET WEIGHT
19MAY 23JUN 07JUL 21JUL 04AUG 18AUG 02SEP
SACRIFICE DATE

Figure 2.4. Mean otolith radius (um) +/- 1 STD of sacrificed fish by sacrifice date. A: Fish raised under constant light conditions, B: Fish raised under constant dark condtions.

A


1400
1200
1000
800
600
400
200
0
OTOLITH RADIUS
19MAY
23JUN
07JUL
21JUL
04AUG
18AUG
02SEP
SACRIFICE DATE

B

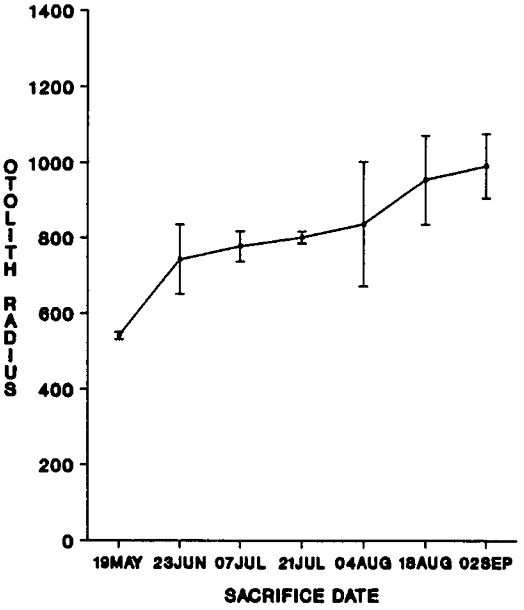
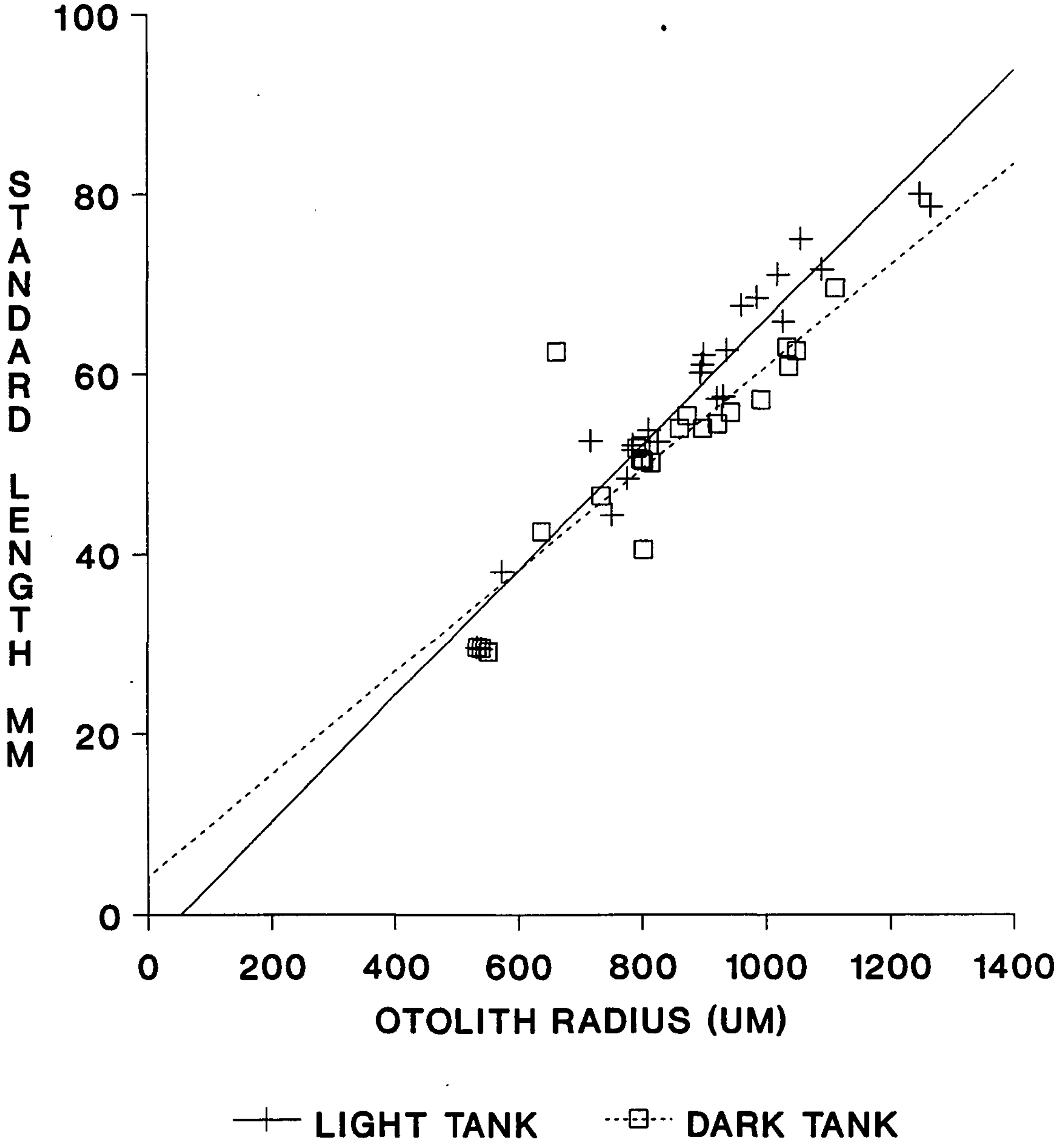

1400
1200
1000
800
600
400
200
0
OTOLITH RADIUS
19MAY
23JUN
07JUL
21JUL
04AUG
18AUG
02SEP
SACRIFICE DATE

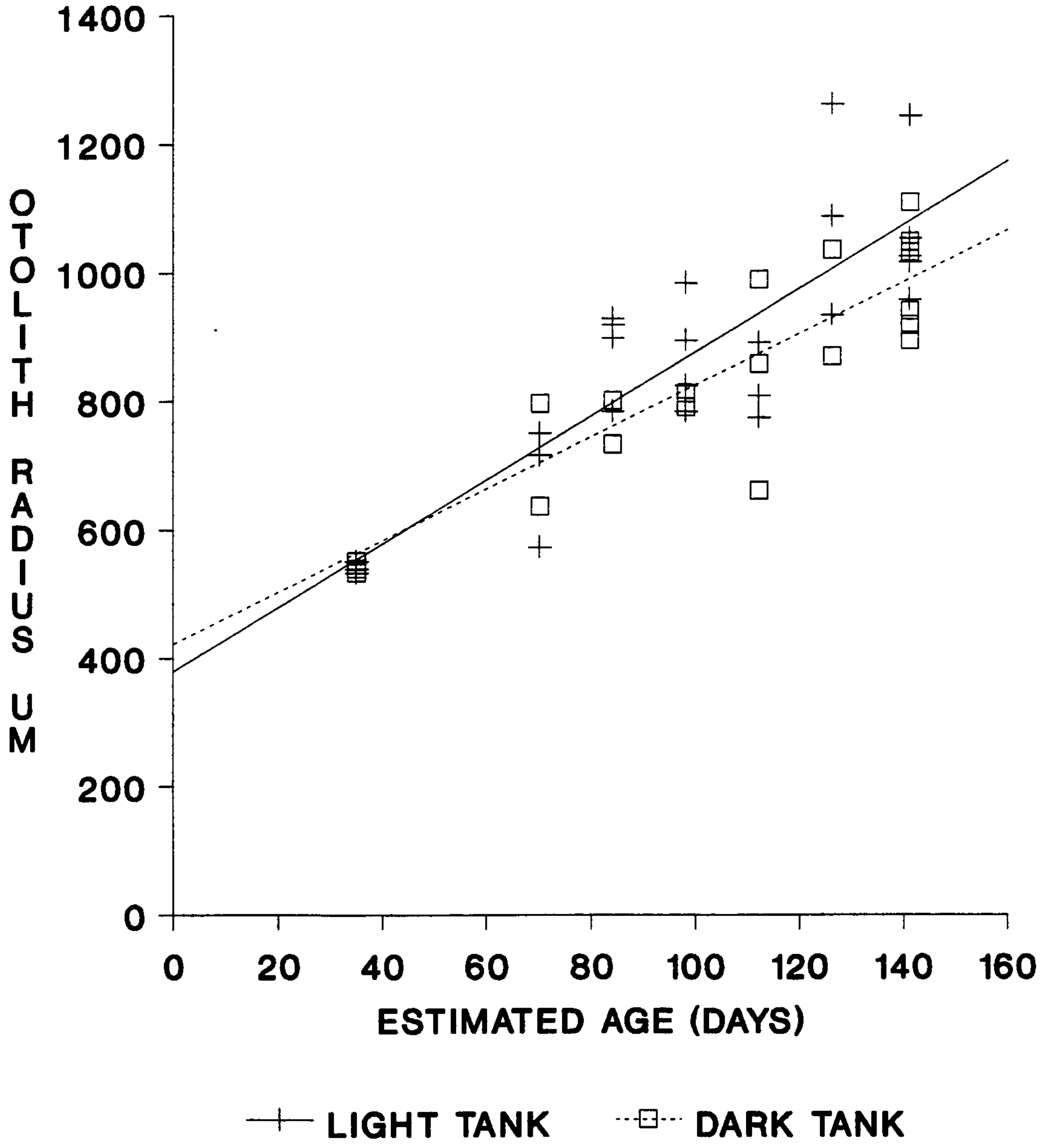
Figure 2.5. Otolith radius-fish length relationships for fish raised under constant light (-x-x-x-) and constant dark (-□-□-□-) conditions .


100
80
60
40
20
0
STANDARD LENGTH MM
0
200
400
600
800
1000
1200
1400
OTOLITH RADIUS (UM)
LIGHT TANK
DARK TANK

had a standard length of 62.4 mm and a much smaller otolith of 662 um, as compared with fish of similar length with otolith radii of 1042 um and 918 um in the dark tank and light tank, respectively. The fish with a standard length of 62.4 mm was known to be 112 days old and had a mean increment count of 96 increments. Two fish sacrificed from the same tank on the same date had mean counts of 94 and 95 growth increments, indicating that the slow growth of the otolith did not affect the deposition of daily increments. A comparison of the otolith-fish length relationships between the light and dark tanks generally indicates that the slower growing fish, raised under constant dark conditions, had larger otoliths than fish of similar size raised under constant light conditions. An ANCOVA analysis showed no significant difference between otolith-fish length relationships for the light and dark tanks (F=1.66, P=0.206). The lack of significance between relationships may have been caused by the one fish sacrificed from the dark tank having a much smaller otolith radius.

The change in otolith radius with age complemented somatic growth rate differences between the tanks (Figure 2.6). The slow growing fish raised in the dark tank had smaller otoliths than the faster growing fish of the light tank, even though fish were the same age. An ANCOVA analysis, however, showed no significant differences in regression equations between tanks (F=2.12, P=0.1545).

Figure 2.6. Otolith radius versus age for fish raised under constant light (-x-x-x-) and constant dark (-□-□-) conditions.


OTOLITH RADIUS UM
0
200
400
600
800
1000
1200
1400
0
20
40
60
80
100
120
140
160
ESTIMATED AGE (DAYS)
LIGHT TANK
DARK TANK

DAILY DEPOSITION

Fish sacrificed on May 19 before the start of the experiment had a mean increment count of 35.7 (Table 2.1 and 2.2), which is not significantly different from the known age of 35 days, indicating daily deposition of growth increments. Underestimation of ages from daily growth increments was not apparent until late July to early August in both the light (Table 2.1) and dark tanks (Table 2.2), as seen from the low mean increment counts and a range of values that does not overlap the known age. The standard deviation of increment counts increases with sampling date in 1987, indicating much greater variability in counts with progression of the experiment. In 1989, standard deviations appeared to remain more constant.

Linear regression equations of mean increment count versus known age were calculated for data from May 19 through September 2, from May 19 through August 18, and from May 19 through July 21 to determine when deposition of increments ceased to be on a daily basis (Table 2.3). A slope not significantly different from one indicates daily deposition of growth increments. Data from 19 May-2 September and 19 May-18 August showed slopes significantly different from one in both the light and dark tanks. The intercept was not significantly different from zero for either equation in the light tank, but was significantly different from zero in the dark tank. Data from the both the light and dark tanks had

Table 2.1. Descriptive statistics of growth incrment counts for sacrificed juvenile striped bass raised under constant light conditions in the laboratory.

SACRIFICE DATE	N	KNOWN DAYS	MEAN	STD	RANGE
19 MAY	3	35	35.7	0.76	35.0 - 36.5
23 JUNE	3	70	71.3	2.47	69.5 - 73.0
02 JULY	2	84	82.2	0.29	82.0 - 82.5
21 JULY	2	98	97.8	1.06	97.0 - 98.5
04 AUGUST	2	112	98.0	1.41	97.0 - 99.0
18 AUGUST	2	126	117.8	3.89	115.0 - 120.5
02 SEPTEMBER	3	141	121.5	3.04	118.0 - 123.5

Table 2.2. Descriptive statistics of growth increment counts for sacrificed juvenile striped bass raised under constant dark conditions in the laboratory.

SACRIFICE DATE	N	KNOWN DAYS	MEAN	STD	RANGE
19 MAY	3	35	35.7	0.76	35.0 - 36.5
23 JUNE	3	70	68.5	1.80	67.0 - 70.5
07 JULY	2	84	81.0	6.36	76.5 - 85.5
21 JULY	4	98	93.5	5.80	89.0 - 102.0
04 AUGUST	1	112	100.5	----	--------
18 AUGUST	3	126	118.8	6.53	112.0 - 125.0
02 SEPTEMBER	3	141	131.5	11.26	120.0 - 142.5

Table 2.3. Linear regression equations and tests of significance for juvenile striped bass raised under constant light and dark conditions in the laboratory. Equations were calculated for all data in each tank and for truncated data sets. (** = P < 0.01, * = P < 0.05, NS = not significant).

TANK	SACRIFICE DATES	REGRESSION EQUATION	R-SQ	N	P(SLOPE=1)	P(INT=0)
LIGHT	19MAY-02SEP	Y= 4.79+0.90X	0.97	19	0.0148*	0.2127NS
	19MAY-18AUG	Y= 4.65+0.90X	0.98	16	0.0166*	0.1762NS
	19MAY-21JUL	Y= 3.75+0.92X	0.98	12	0.1508NS	0.3132NS
DARK	19MAY-02SEP	Y=11.23+0.81X	0.98	17	0.0001**	0.0042**
	19MAY-18AUG	Y= 7.18+0.87X	0.98	14	0.0051**	0.0482**
	19MAY-21JUL	Y= 1.78+0.97X	0.99	10	0.2004NS	0.2589NS

a slope not significantly different from one and an intercept not significantly different from zero when data was truncated to July 21. This indicates that daily deposition of growth increments occurred for a total of approximately 100 days, with 60 days being under constant photoperiod.

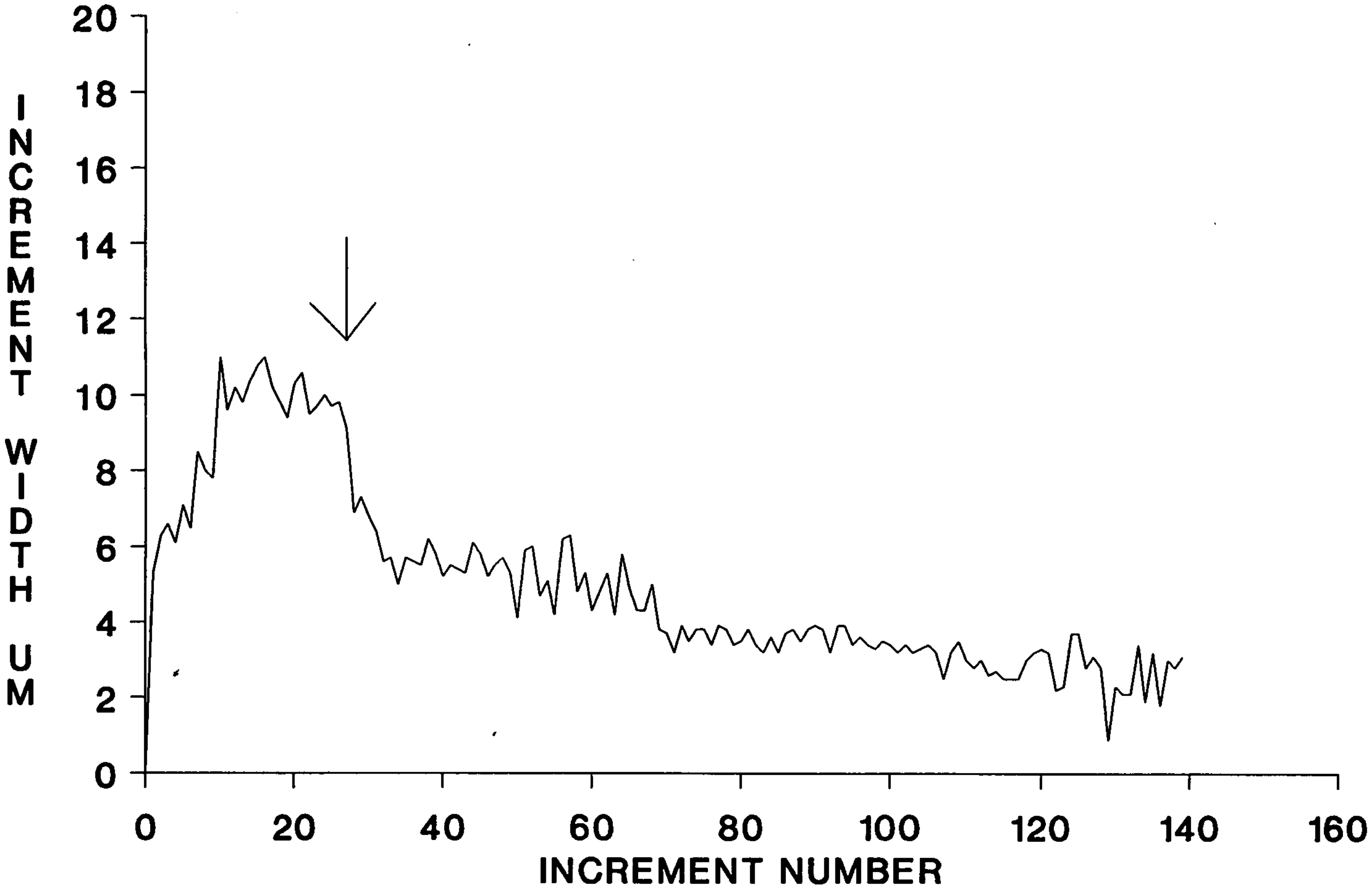
An ANCOVA analysis comparing the linear regressions of mean increment count versus known age from May 19 to July 21 showed no significant difference between the light and dark tanks (F=1.99, P=0.182).

STRESS PERIOD

During processing of otoliths from fish sacrificed from both tanks, it was observed that a distinct opaque zone was present on all otoliths at approximately the same location when viewed under reflected light. Examination of several hundred otoliths from field collected juvenile striped bass showed no opaque zones on any of the otoliths. Therefore, it was postulated that this zone may have been the result of stress induced by shipping and handling, or of acclimation of fish to the experimental design. The opaque zone on fish otoliths is caused by the packing of approximately 10 extremely narrow daily growth increments, which causes a density difference when compared to the translucent zone.

Widths of each growth increment on each otolith were measured with the BIOSONICS Optical Pattern Recognition System. Mean increment width +/- 1STD was then plotted against increment number for fish sacrificed on September 2 (Figure 2.7). Mean increment widths ranged from 2-10 um, with widths increasing from 5.3 um at 1 day to 11.0 um at 10 days of age. From 10 to 30 days increment widths remained relatively constant at approximately 10 um. A sharp decrease in increment widths occurred from 9.2 um at 30 days to 5.7 um at 36 days, before again reaching a constant value of approximately 5-6 um. At 63 days of age, increment widths decreased to 3.5 um and remained between 0.8 and 3.5 um for the duration of the experiment. It is important to note that these striped bass were shipped from the Fish Hatchery at 30 days of age, which corresponds to the period of decreasing increment widths. Shipping/handling stress, combined with acclimation to the tanks, may have caused a change in the relationship between the opaque and translucent zones of the otolith, thereby causing a stress mark to be observed. This stress mark may be a function of a change in somatic growth rate of the fish during this period.

Figure 2.7. Mean increment widths for all fish from both the light and dark tanks sacrificed on September 2. Arrow marks the rapid decrease in increment widths occurring at 30 days of age.



INCREMENT WIDTH UM
20
18
16
14
12
10
8
6
4
2
0
0
20
40
60
80
100
120
140
160
INCREMENT NUMBER

DISCUSSION

Daily growth increments were deposited on the otoliths of juvenile striped bass for 98 days, with 63 daily increments being deposited during the experimental conditions. Fish held under constant light and constant dark showed no significant difference from a deposition rate of one increment/day for 63 days. After 63 days under experimental conditions the rate of deposition decreased to an average of 0.85 increments/day in the light tank and 0.87 increments/day under constant dark, which was significantly different from a slope of one. These results suggest that daily deposition of growth increments in juvenile striped bass is under the control of an endogenous circadian rhythm. The free-run phase of the rhythm maintained daily deposition for 63 days, before beginning to deviate from a 24-hr periodicity. A new average periodicity of approximately 0.86 increments/day was reached after 63 days and was maintained for an additional 43 days. Due to the 2-week time interval between sacrifice dates, only an average periodicity could be estimated, and it was not possible to determine if this deviation occurred in constant increments on a daily basis. However, an average periodicity of approximately 0.9 increments/day, maintained for over 43 days (from day 98 to day 141), suggests that an endogenous circadian rhythm is the cause of daily increment deposition in juvenile striped bass.

These results are consistent with Rosa and Re (1985) and Re and Rosa (1986), who found continued daily deposition of growth increments in Tilapia mariae and Dicentrarchus labrax, respectively, raised under constant light conditions. Mugiya (1987) found daily deposition in otoliths of larval Salmo gairdneri under both constant light and constant dark. They pointed out, however, that faint fluctuations in uncontrolled variables, such as noise or vibrations, may have influenced their results. Campana and Neilson (1982) and Neilson and Geen (1982) also provided evidence that daily deposition is maintained during constant photoperiods; however, they suggested that a prior period of acclimation to a natural photoperiod is necessary to entrain the endogenous rhythm. Recently, Campana (1984A) showed that if a constant photoperiod is present at hatch, the endogenous rhythm of daily deposition only becomes apparent after an acclimation period of 2-4 weeks. He also found an acclimation period when fish were transferred from a natural light cycle to constant light conditions. No such acclimation period was found for juvenile striped bass after transfer to constant photoperiods in this study.

Constant photoperiod conditions appeared to have an effect on the distinctness of growth increments, with darker increments being deposited during the first 32 days when fish were raised under natural conditions at the hatchery. Re and Rosa (1986) also found more distinct discontinuous zones under natural photoperiods than under constant light conditions. Jones and Brothers (1987) found a similar effect caused by starvation of striped bass. The fact that they found continued daily deposition of growth increments in intermittently starved striped bass suggests that natural cycling of environmental factors (photoperiod, temperature, and feeding) does not have a direct effect on deposition rate, but may effect the resolution of growth increments.

Geffen (1982) suggested that daily deposition of growth increments was directly related to somatic growth of the fish. No relationship between deposition rate and somatic growth was found during these experiments (Chapter I). Somatic growth in both length and weight was approximately 50% slower in fish raised in constant dark; however, deposition of daily increments was not significantly different between the light and dark experiments. One fish, sacrificed at a length of 62.4 mm and an age of 112 days, had an otolith radius 30-40% smaller than fish of similar size. This fish had the same number of otolith increments as 2 other fish sacrificed on the same date, indicating that slow growth of the otolith does not affect the rate of increment deposition.

The relationship between somatic growth of the fish and otolith growth was linear for both experimental conditions.

However, slower growing fish raised under constant dark had larger otoliths than similar sized, faster growing fish raised under constant light. This study indicates that the otolith continues to grow with age of the fish, even when somatic growth of the fish decreases. Similar observations were made by Secor and Dean (1989) and Secor et al. (1989) for striped bass. Reznick et al. (1989) and Mosegaard et al. (1988) also found inconsistent otolith-fish length relationships for guppies and Arctic char, respectively.

Secor and Dean (1989) proposed a model to explain these discrepancies. They suggested that a minimum amount of calcium carbonate is deposited in the form of a daily increment, whether the fish is growing or not. At faster somatic growth rates an additional amount of calcium carbonate is deposited in addition to this minimum. Therefore, after a period of time in which individual growth rates diverge, the otolith of the slower growing fish may eventually reach a larger size than the faster growing fish, even though fish are similar in length. The results of the otolith-fish length relationships for fish raised under constant light and constant dark support this theory of otolith growth.

A stress mark, in the form of a rapid decrease in increment widths, was found on all otoliths. This mark corresponds with the period of shipping and the first week of acclimation to the experimental design. It can be reasonably assumed that somatic growth of fish decreased during this period, lending credence to Secor and Dean's (1989) model of minimal deposition of calcium carbonate during periods of slower somatic growth, as compared with fast somatic growth periods. Victor (1982) produced a mark composed of 5 unusually wide increments through supplemental feeding, which would have caused an increase in somatic growth of the fish. A similar decrease in mean increment widths was observed for field-collected juvenile striped bass (Chapter III), however, no distinct opaque zone was observed in any of the otoliths from these fish. These results suggest that maximum growth of juvenile striped bass may occur from 0-30 days. The stress of shipping and handling in the present study, combined with a normal decrease in somatic growth at 30 days of age, may have caused the opaque zone do be observed in all otoliths analyzed in this study.

The correspondence of average increment widths with average somatic growth and the change in increment width with periods of stress or increased feeding, suggests that measurements of increment width may represent average changes in growth of the fish. Wilson and Larkin (1982) found a strong positive relationship between mean widths of daily growth increments and a mean daily change in body weight of sockeye salmon fry. Gutierrez and Morales-Nin (1986) suggested that otolith growth was a conservative process influenced by environmental conditions at the time of deposition and also a memory of previous growth. Secor and

Dean (1989) and Campana (1984B) found a lagged effect of feeding rate on increment widths.

The results presented provide evidence that daily deposition of growth increments is under the control of an endogenous circadian rhythm, and is not affected by either somatic growth of the fish or growth of the otolith. Therefore, application of otolith-derived ages to growth, mortality, and spawning frequency studies appears to be valid. The relationship between somatic and otolith growth in juvenile striped bass was linear under the experimental conditions of this study. However, a great deal of variability existed in this relationship for the individual fish studied. Variations in the otolith radius-fish length relationships based on somatic growth rate differences may cause problems when applying the back-calculation technique to juvenile striped bass, even though under natural conditions, closely associated river systems would have similar controlling factors on growth. Variations in growth rates of individual fish may cause an inconsistent otolith radius-fish size relationship, even under natural conditions. Therefore, otolith-fish length relationships for natural populations of striped bass must be examined closely before attempting to reconstruct growth histories of individual fish.

The fact that mean increment widths correspond to mean growth rates may suggest that the back-calculation technique is valid over longer time periods (approximately 2-week intervals) and may provide an average growth history of all fish collected.

Chapter III - Population dynamics of juvenile striped bass populations in Virginia river systems.

INTRODUCTION

Contemporary fisheries research involving the daily increment aging technique have emphasized the application of otolith-derived ages examining growth, survival, and recruitment dynamics. Enumeration of daily increments provides a method of estimating population growth rates (Crecco and Savoy 1985; Lough et al. 1982; Penney and Evans 1985; Rosenberg and Haugen 1985; Struhsaker and Uchiyama 1976; Townsend and Graham 1981; and Warlen and Chester 1985), spawning frequencies (Miller and Storck 1984; Radtke and Dean 1982; Rice et al. 1987; and Warlen 1988), mortality and survival (Crecco et al. 1983; Crecco and Savoy 1985; Essig and Cole 1986; and Rosenberg and Haugen 1982), migration and settlement (Deegan and Thompson 1987; Victor 1982; and Warlen and Chester 1985), and individual growth histories (Bradford and Geen 1987; Marshall and Parker 1982; Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; and Secor et al. 1989).

Striped bass have historically been an important commercial and recreational fisheries species in the mid-Atlantic bight. Drastic declines in abundance in the late-70's and early 80's forced the enactment of strict conservation measures to protect residual striped bass adult stocks. High production levels of juveniles in Maryland in 1989 (Maryland Department of Natural Resources, unpublished data) have produced the three-year running average of 8 defined by Amendment #3 of the Interstate Management Plan for Striped Bass as the trigger to reopen the striped bass fisheries (Atlantic States Marine Fisheries Commission 1981). High juvenile striped bass indices were also produced in Virginia in 1987, 1988, and 1989 (Virginia Institute of Marine Science, unpublished data).

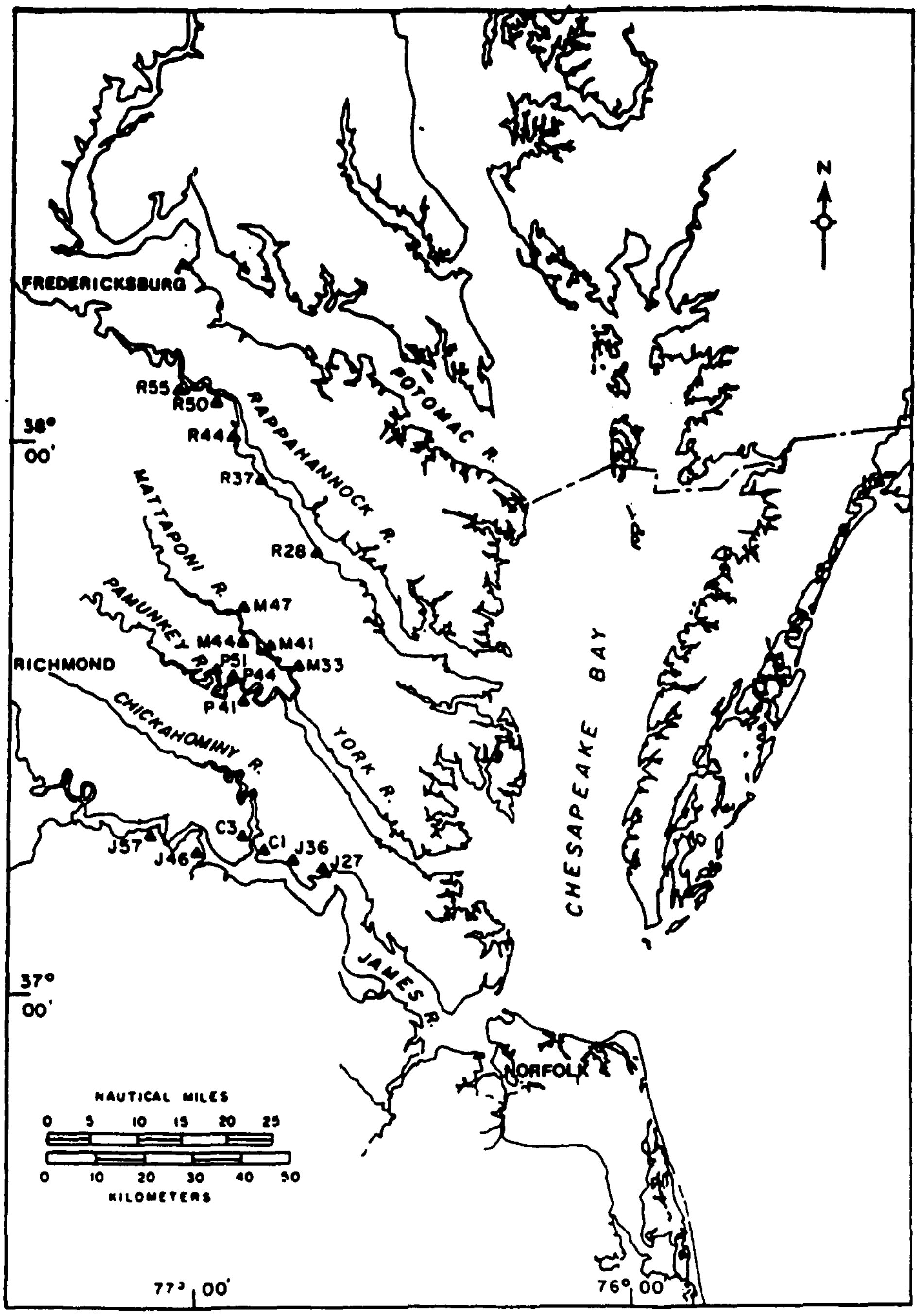
Striped bass populations are characterized by the occasional production of dominant year classes. There is relatively little information on the factors responsible for the production of a dominant year-class, however, it is generally agreed that density-independent environmental factors during the first year of life are important determinants of subsequent year-class strength (ASMFC 1981; Polgar 1931). The interaction of differential growth and mortality may be a major factor controlling year-class strength in striped bass.

The use of the otolith aging technique to provide more accurate estimates of growth and survival may facilitate greater knowledge of recruitment processes, leading to a better understanding of dominant year-class production in striped bass. This study was primarily designed to compare estimates of population growth rates, mortality, and abundance of two year-classes of juvenile striped bass in four Virginia river systems.

MATERIALS AND METHODS

Juvenile striped bass were collected in 1986 and 1987 with a 100' 1/4" mesh bagless seine in the James, Rappahannock, Mattaponi, and Pamunkey Rivers, which are Virginia tributaries of the Chesapeake Bay (Figure 3.1). All rivers have been documented as being major spawning rivers for striped bass (Tresselt 1950; and Austin 1980). Collections were made in conjunction with the Virginia Institute of Marine Science juvenile striped bass seine survey. Survey sampling stations included 6 stations in the James River (river mile 27-57), 5 stations in the Rappahannock (river mile 28-55), 4 stations in the Mattaponi (river mile 33-47), and 3 stations in the Pamunkey (river mile 41-51). Salinity ranged from 0 to 12.2 ppt, and temperature ranged from 23.0 to 33.5 C in both years of collection. Auxiliary stations were included in the sampling design when it was observed that the survey stations did not include the entire distributional range of juvenile striped bass in these year-classes. Auxiliary stations were added to the James and Rappahannock Rivers in 1986 to extend sampling 2 miles above the upper survey station and 3-7 miles below. The survey sampling design in 1987 was similar to 1986, however, auxiliary stations were added to all

Figure 3.1. Map of the Chesapeake Bay showing juvenile striped bass sampling stations in the James, Rappahannock, Mattaponi, and Pamunkey Rivers.


N
FREDERICKSBURG
POTOMAC R.
RAPPAHANNOCK R.
R55
R50
R44
R37
R28
38°
00'
MATTAPONI R.
M47
M44
M41
M33
PAMUNKEY R.
P51
P44
P41
RICHMOND
CHICKAHOMINY R.
YORK R.
C3
C1
J57
J46
J36
J27
JAMES R.
CHESAPEAKE BAY
37°
00'
NORFOLK
NAUTICAL MILES
0 5 10 15 20 25
0 10 20 30 40 50
KILOMETERS
77° 00'
76° 00'

rivers due to an extension of the distributional range. Auxiliary stations extended the sampling design up to 10 miles below the lower station and up to 18 miles above.

All fish were sacrificed from collections of less than 25 individuals, while a random subsample of 25 fish was taken at stations with larger collections. Striped bass were preserved in 10% formalin for 1 day, rinsed with water (2 changes) for 3-4 days, and transferred to 45% buffered isopropanol alcohol until removal of otoliths. Standard, fork, and total lengths were measured (+/- 0.1 mm), and fish wet weights were taken (+/- 0.1 g). Otoliths were removed and stored dry in tissue culture trays. Stomachs were removed and combined taxa were wet weighed (+/- 0.001 g). Average stomach fullness was calculated from all fish to qualitatively assess the availability of food to fish within each population.

Sagittal otoliths were processed in the transverse section as described in Chapter I. Calculated ages were increased by 3 increments to adjust for the delay in first increment deposition and by employing a correction factor to fish >80 days, as determined from the validation phase of this study (Chapter I). Birthdates were determined by subtracting the estimated age of each fish from the collection date. Data were then pooled for weekly intervals within each river and year-class. Population growth rates for fish collected from 1 June-30 August (approximately 30-110 days old) were variously calculated: 1) as the slope of the regression of standard length on estimated age, 2) from length-frequency modal progression, and 3) by employing an assumed common hatch date of April 15. April 15 was chosen as the date of peak spawning from historical egg surveys conducted at the Virginia Institute of Marine Science in 1980-1983 (Olney et al. 1985). Egg and larval studies were not conducted in 1986 and 1987; therefore, there is no direct evidence for peak spawning on April 15 in these years. Average condition factors and allometric coefficients were calculated for each river in each year. Mortality estimates were calculated from an age-based catch-curve analysis (Essig and Cole 1986). To calculate mortality, age-at-capture was estimated for all fish collected in each river system from the age-standard length regressions for each separate river population due to the small sample size of aged fish in each system. A catch curve was then plotted for each river population by plotting log frequency versus mean estimated age. Growth, mortality, abundance, and condition of fish were compared on a population basis, and back-calculated birthdate distributions were utilized for comparisons of growth and mortality within hatching cohorts.

RESULTS

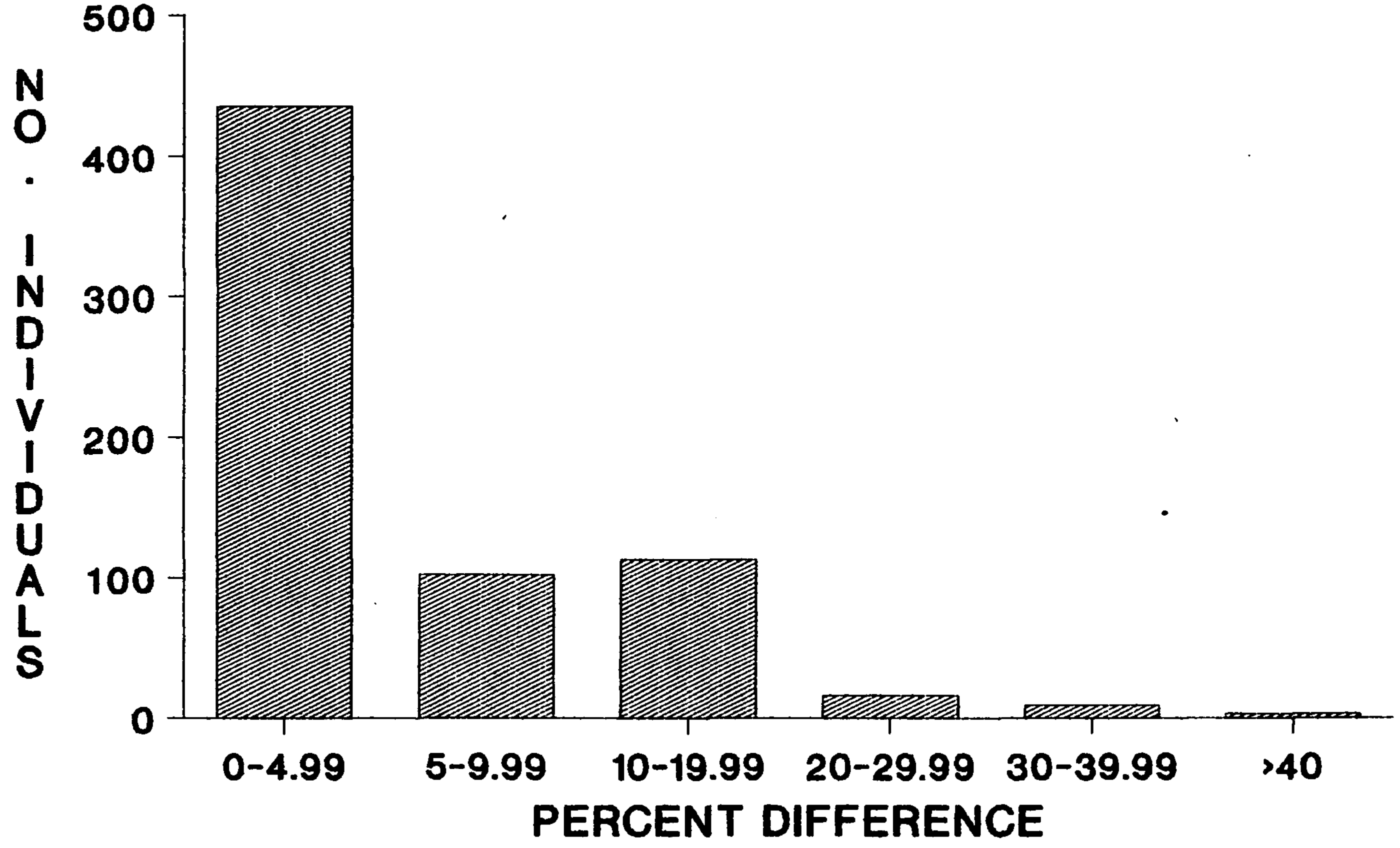
A total of 943 and 1752 striped bass were collected from July - September in 1986 and 1987, respectively (Appendix I). Subsamples for otolith analysis were selected by a stratified random sampling design based on 10mm size classes. All fish from the lower and upper size ranges, which tended to be relatively underrepresented in the samples, were analyzed so as to guarantee inclusion of the entire size and age distribution.

A total of 678 otoliths were processed, however, only 542 (80%) had a percent difference between increment counts of less than 10 per cent, and were included in the analysis (Figure 3.2). Of these, 435 (80%) had a percent difference between readings of less than 5 per cent. Twenty-eight otoliths had a percent difference greater than 20 per cent, with 19 of these being from fish sacrificed in September.

The structure of wild striped bass otoliths was consistent with the description of otoliths of hatchery-reared fish (Chapter I). Twelve of the otoliths (2.2%) were observed to contain two primordia within the nucleus, howver, this did not interfere with counting of daily growth increments. Vateritic otoliths were observed in 0.6% (3 of

Figure 3.2. Histogram of the per cent difference between two readings of each otolith. Only fish with less than 10% difference were included in the analysis (542 fish).

MEAN PERCENT DIFFERENCE



536) otoliths analyzed. Daily increment deposition was not present in the vateritic portion of these otoliths.

LENGTH-WEIGHT RELATIONSHIPS

Length-weight relationships were calculated for each separate river population in 1986 and 1987 (Table 3.1). Coefficients of determination of the log transformed data were greater than 0.97 in all rivers. Allometric coefficients, calculated as the slope of the log transformed length-weight regression, ranged from 2.63 to 3.13.

An ANCOVA analysis comparing all rivers in the separate years showed a significant difference between length-weight relationships, separating the rivers into two groups (P=0.235). The James, Mattaponi, and Rappahannock Rivers in 1986 and the Mattaponi and Pamunkey Rivers in 1987 formed the group with the lower allometric coefficients (2.62-2.92), while the Pamunkey River in 1986 and the James and Rappahannock Rivers in 1987 formed the group with the higher allometric coefficients (3.11-3.13).

CONDITION FACTOR AND STOMACH FULLNESS

Relative condition factor was calculated for each river in each year from the equation $K=W/L^b * 10000$ (LeCren 1951), where W = wet fish weight, L = standard length, and b = the population allometric coefficient. Average condition factors ranged from 0.0170 in the Rappahannock River in 1986 to 0.0190

Table 3.1. Juvenile striped bass length-weight relationships (where Y=log(standard length) and X=log(wet weight)), coefficient of determination for the relationship, average annual condition factor, and average annual stomach fullness for each separate river population in 1986 and 1987. Ranges of average annual condition factor and average annual stomach fullness are shown in parentheses.

YEAR	RIVER	N	REGRESSION EQUATION	R-SQ	AVE. COND. FACTOR	AVE. STOM. FULLNESS
1986	JAMES	506	$Y=4.64+2.93X$	0.97	0.0176 (0.0102-0.0316)	136.66 (1.79-1180.87)
	RAPP	292	$Y=4.14+2.63X$	0.98	0.0170 (0.0074-0.0277)	89.40 (3.47-948.06)
1987	JAMES	461	$Y=4.94+3.11X$	0.99	0.0175 (0.0113-0.0227)	117.17 (4.26-1378.18)
	RAPP	793	$Y=4.96+3.13X$	0.99	0.0180 (0.0074-0.0230)	115.84 (4.72-8867.26)
	MATT	241	$Y=4.42+2.80X$	0.99	0.0190 (0.0126-0.0408)	174.09 (0.78-1152.62)
	PAM	267	$Y=4.52+2.87X$	0.99	0.0189 (0.0091-0.0315)	173.81 (5.24-1178.90)

in the Mattaponi River in 1987, with individual condition factors ranging from 0.0074 to 0.0408 (Table 3.1).

Average annual stomach fullness ranged from a low value of 89.40 in the Rappahannock River in 1986 to 174.09 in the Mattaponi River in 1987 (Table 3.1). Ranges of stomach fullness for individual fish were extremely large, ranging from 0.78 to 8867.26.

BIRTHDATE DISTRIBUTIONS

The Mattaponi and Pamunkey Rivers in 1986 were not included in the analysis of birthdate distributions due to small sample sizes. Separate birthdate distributions were plotted for the months of July, August, and September in the James and Rappahannock Rivers in 1986 (Figures 3.3 A-C and 3.4 A-C). These plots show that there was a one week shift in the mode of the distributions from July to August and a one-two week shift in the range of the distributions in both rivers. The birthdate distributions calculated for fish collected in September have a mode occurring in early June and an extension of range into late June. The shift in peak birthdate occurring in the September samples in both rivers appears to be due to an underestimation of ages, possibly caused by a decrease in resolution of narrower increments near the edge of the otolith. All fish collected in the month of September were deleted from further analysis due to the uncertainties involved in aging these fish. The one week shift in mode and

Figure 3.3. Birthdate distributions for the James River in 1986 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: September samples, and D: Pooled July and August samples.

JAMES RIVER 1986

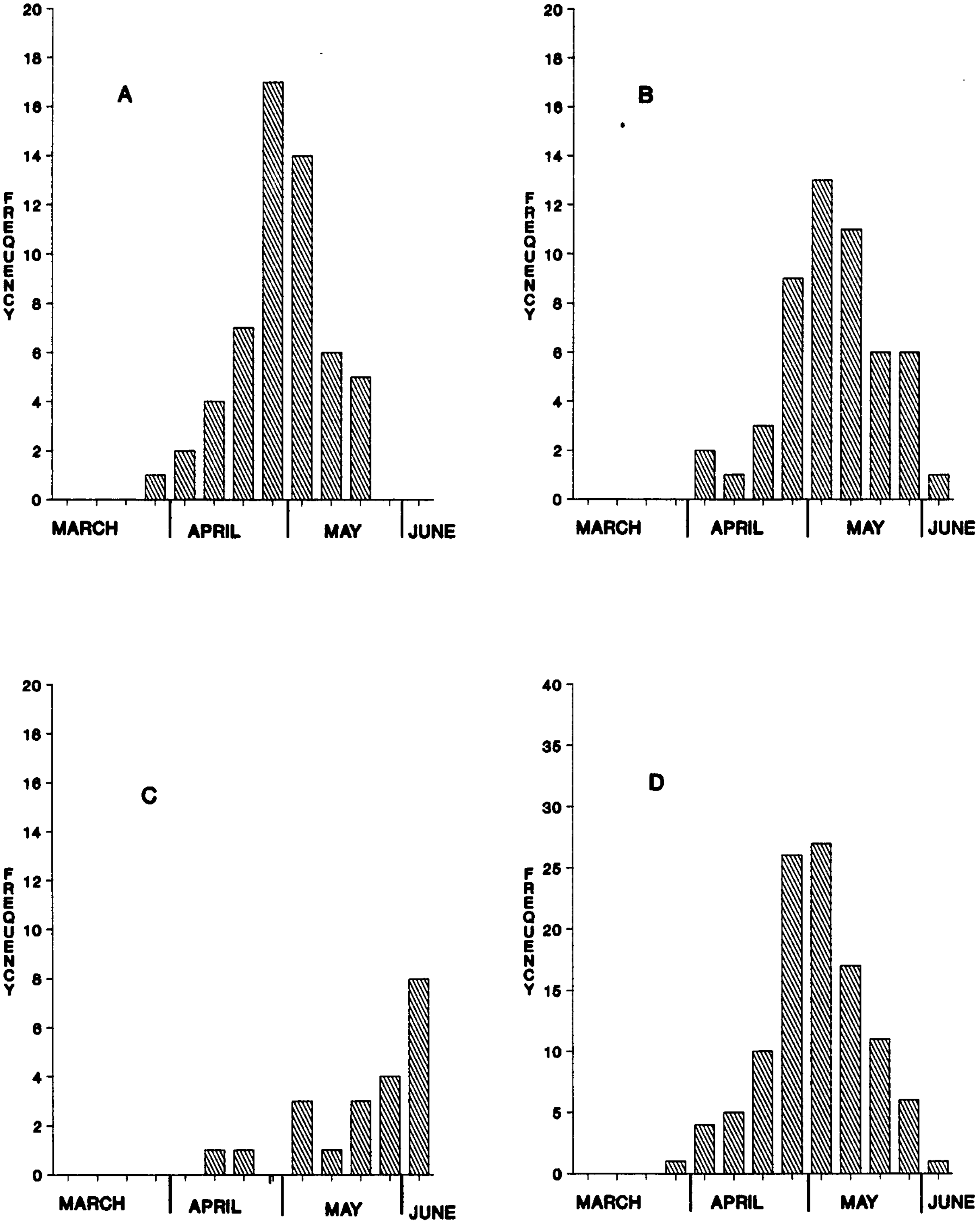
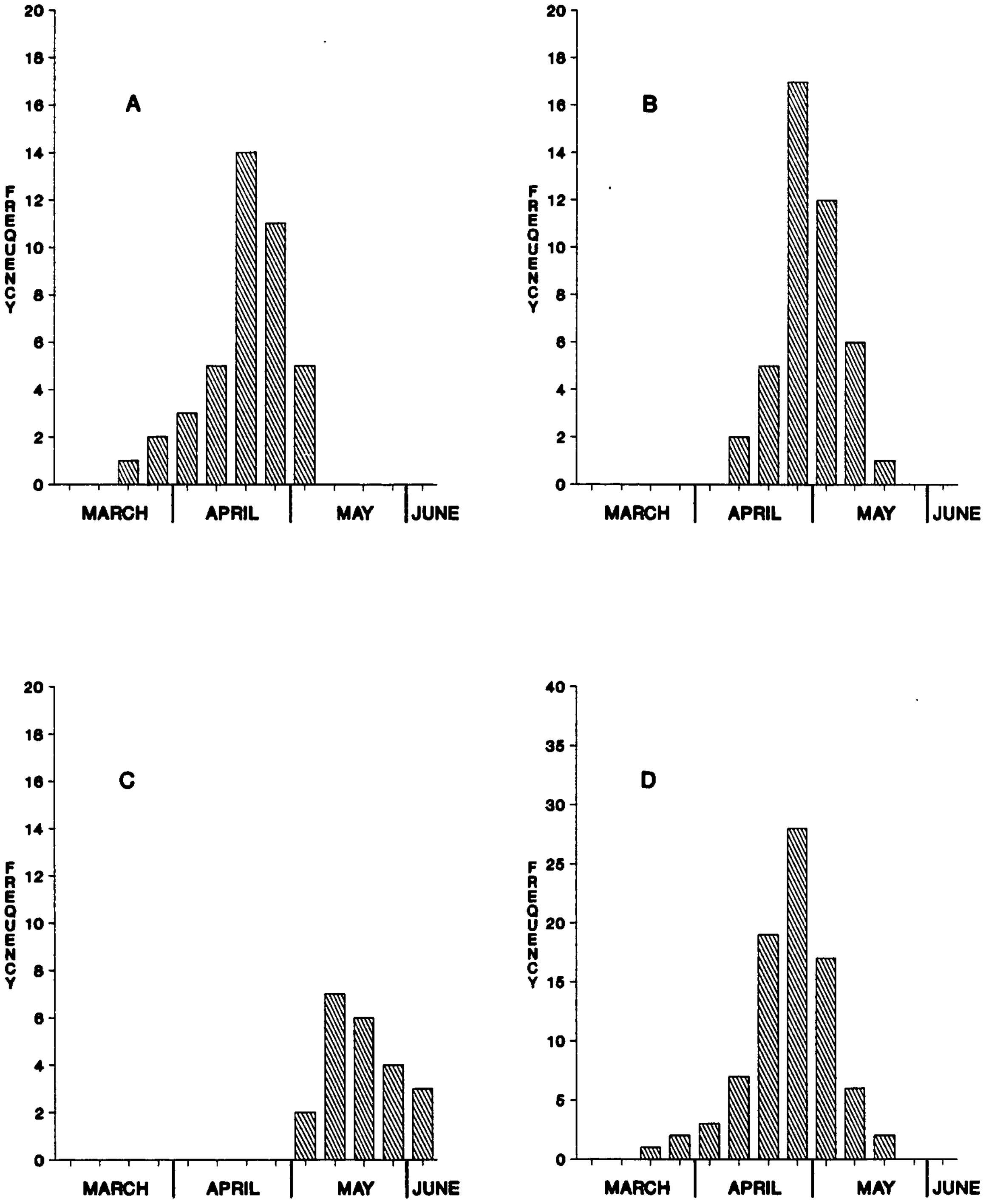


Figure 3.4. Birthdate distributions for the Rappahannock River in 1986 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: September samples, and D: Pooled July and August samples.

RAPPAHANNOCK RIVER 1986



range of birthdates from the July to the August samples in both rivers may be due to a slight underestimation of ages of fish collected later in the sampling season, due to differential mortality of fish hatched earlier in the season, or due to daily increment deposition becoming less than daily, possibly caused by declining water temperatures in early fall.

A total of 10 fish from each month (July-September) were analyzed with the scanning electron microscope to determine if underestimation of increments may have occurred due to resolution limits of light microscopy (Table 3.2). A paired T-test analysis on each separate month showed a significant difference between increment counts from the two techniques, with SEM providing lower counts for all otoliths ($P<0.0001$). Enumeration of increments using SEM appears to be unreliable for juvenile striped bass otoliths, due to the convolutions inherent in these larger otoliths and the inability to focus on all increments with the SEM. Therefore, it was impossible to determine if an underestimation problem with the light microscope counts caused the shift in the birthdate distributions.

Birthdate distributions for the James and Rappahannock Rivers in 1986 were then calculated from the pooled July and August samples (Figures 3.3 D and 3.4 D). Distributions for both rivers appeared to be normally distributed, with modes occurring in the first week of May in the James River and the

Table 3.2. Comparison of mean otolith increment counts made using a light microscope and a scanning electron microscope for juvenile striped bass collected in 1986.

MONTH OF COLLECTION	LIGHT MICROSCOPY COUNT	MEAN SEM COUNT
JULY	68.5	61
	78.0	69
	79.0	72
	81.0	63
	81.0	70
	81.5	59
	82.5	74
	82.5	74
	83.0	73
	84.0	73
AUGUST	88.0	68
	89.5	72
	90.0	71
	91.5	70
	92.5	69
	93.0	51
	94.0	71
	94.5	79
	100.5	75
	104.5	91
SEPTEMBER	90.0	62
	90.0	62
	97.0	87
	97.5	68
	103.5	74
	104.5	71
	105.5	64
	107.5	73
	116.0	90
	133.5	115

last week of April in the Rappahannock River. Fish hatched from the last week of April to the first week of May accounted for 73.9 and 81.9 per cent of all fish in the James and Rappahannock Rivers, respectively. The range of birthdates was from the last week of March to the first week of June in the James River, and from the second week of March to the third week of May in the Rappahannock River.

Birthdate distributions were also calculated for separate months for each river in 1987. September samples were not included in this analysis due to the aging difficulties apparent in the 1986 data. There was no apparent shift in the mode or range of the distributions from the July to the August samples in any of the four rivers studied in 1987 (Figures 3.5-3.8 A and B). Several possibilities for this difference relative to the 1986 data are possible. First, there may have been an underestimation of ages of fish collected in August in the 1986 data, with no underestimation in 1987. This appears unlikely since all fish in both years were aged under the same criteria. Secondly, differential mortality by size-classes may have occurred in 1986 but not in 1987. Chapter IV, however, provided evidence that 'reverse' Lee's phenomenon occurred in the James River in 1987, implying that size-selective mortality occurred in this river. Therefore, this hypothesis does not appear to be valid. The third, and most reasonable, possibility is that the smaller range of

Figure 3.5. Birthdate distributions for the James River in 1987 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: Pooled July and August samples.

JAMES RIVER 1987

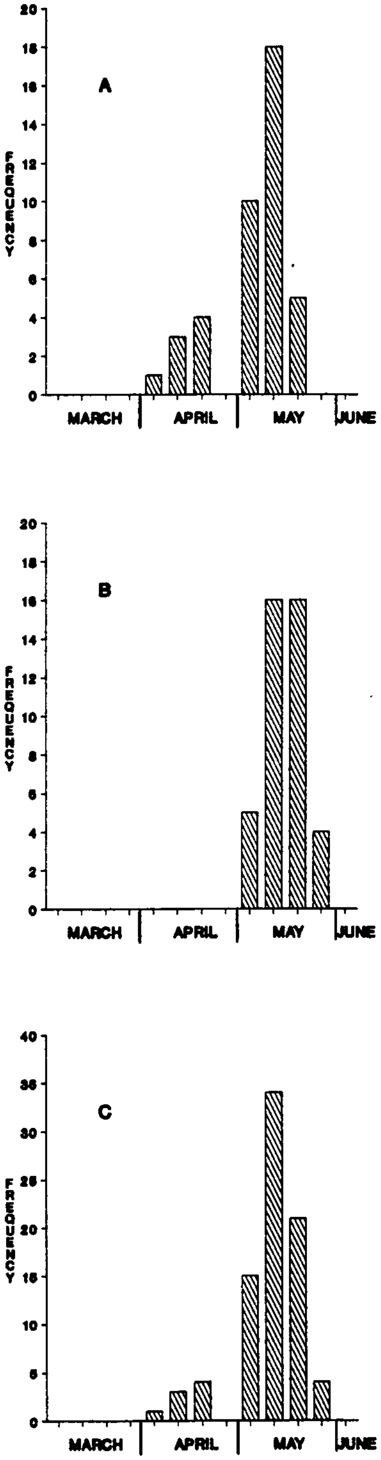


Figure 3.6. Birthdate distributions for the Rappahannock River in 1987 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: Pooled July and August samples.

RAPPAHANNOCK RIVER 1987

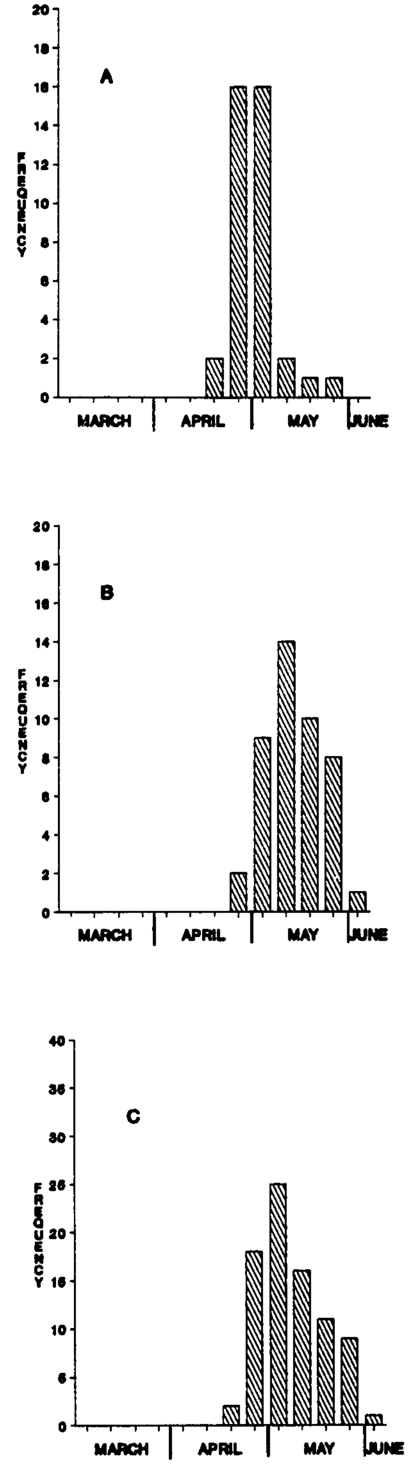


Figure 3.7. Birthdate distributions for the Mattaponi River in 1987 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: Pooled July and August samples.

MATTAPONI RIVER 1987

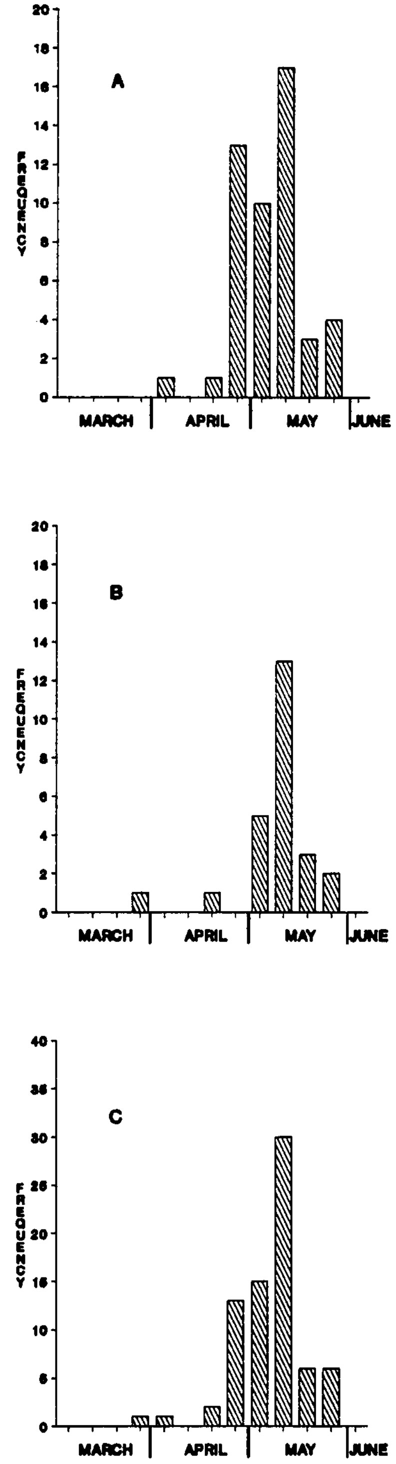
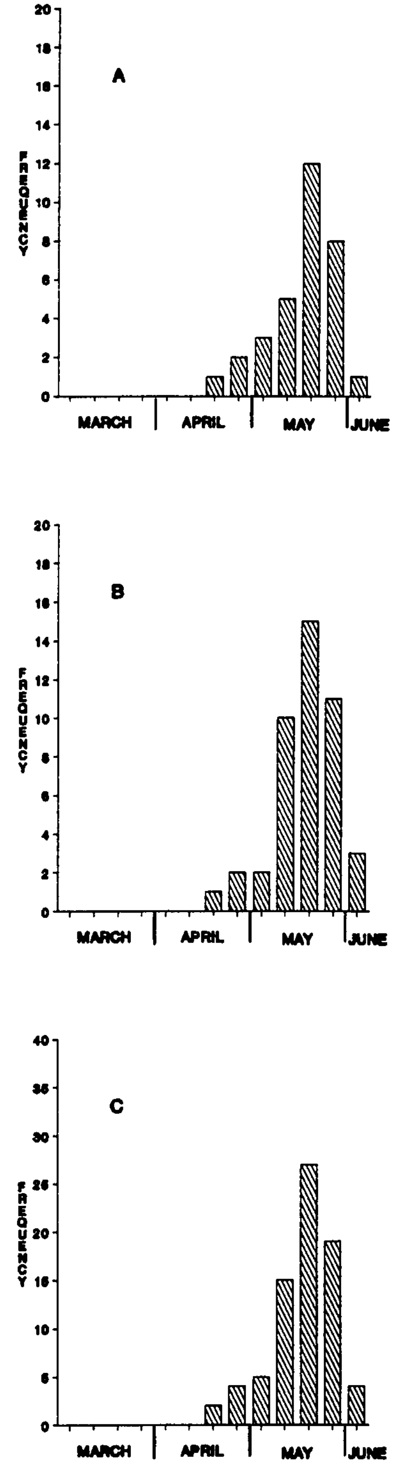


Figure 3.8. Birthdate distributions for the Pamunkey River in 1987 with birthdates pooled over weekly periods. A: July samples, B: August samples, C: Pooled July and August samples.

PAMUNKEY RIVER 1987



birthdates in the 1987 samples does not allow the shift in mode and range to be apparent.

The distribution of birthdates in all rivers in 1987 calculated from the pooled July and August samples was skewed to late in the season with a mode in all rivers occurring in the month of May (Figures 3.5-3.8 C). The range of birthdates was from the first week of April to the last week of May in the James River, from the second week of April to the first week of June in the Rappahannock and Pamunkey Rivers, and from the last week of March to the last week of May in the Mattaponi River. The slight variations in range of the distributions was caused by a few fish with birthdates early in the season. In all rivers, the majority of fish had birthdates occurring in the month of May (96.2% in the James River, 69.2% in the Mattaponi River, 90.3% in the Pamunkey River, and 93.0% in the Rappahannock River).

GROWTH ANALYSIS

As in the birthdate distributions, the Mattaponi and Pamunkey Rivers in 1986 were not included in the growth rate analysis due to small sample sizes. Growth rates for all other rivers in both years were modelled using linear least-squares analysis. All three methods of growth rate estimation produced significant relationships between either standard length and age or date ($0.0251<P<0.0001$). Coefficients of determination, however, were extremely variable between methods and also between populations. The coefficients of determination ranged from 0.279-0.546 using the otolith technique, from 0.189-0.709 using a common hatch date, and greater than 0.70 in all populations using modal progression (Table 3.3).

Population growth rates calculated with the otolith aging technique were 0.411 and 0.301 mm/day in the James and Rappahannock Rivers in 1986, respectively (Table 3.3). Growth rates calculated for 1987 were 0.437 in the James River, 0.417 in the Rappahannock River, 0.597 in the Mattaponi River, and 0.530 in the Pamunkey River. Growth rates calculated from a common hatch date of April 15 were similar for all rivers in both years (0.290-0.391). Growth rate estimates using this method were lower in all rivers except the Rappahannock River in 1986 as compared to the otolith aging technique. The use of a common hatch date based on spawning frequency or modal birthdate as calculated in the previous section for each population and year-class would increase the reliability of growth rate estimates based on a common hatch date. Growth estimates based on length-frequency modal progression data (Table 3.4) were higher than those calculated from the otolith aging technique in both rivers in 1986, and lower in all rivers in 1987 (Table 3.3). The use of a common hatch date or length-frequency modal progression assumes that all fish were either hatched on the same day or that all fish attain the same average length over time. Neither method considers

Table 3.3. Comparison of growth rate estimates in mm/day calculated by aging juvenile striped bass by daily growth increments, estimation of ages from a common hatch date of April 15, and from length-frequency modal progression. All estimates are for the period 1 June-30 August.

YEAR	RIVER	METHOD	GROWTH RATE	N	R-SQ	PROB.
1986	JAMES	Otolith Technique	0.411	113	0.279	0.0001
		Common Hatch Date	0.290	506	0.189	0.0001
		Modal Progression	0.551	506	0.935	0.0072
	RAPP	Otolith Technique	0.301	82	0.528	0.0001
		Common Hatch Date	0.330	292	0.709	0.0001
		Modal Progression	0.532	292	0.896	0.0530
1987	JAMES	Otolith Technique	0.437	83	0.451	0.0001
		Common Hatch Date	0.377	461	0.450	0.0001
		Modal Progression	0.304	461	0.853	0.0251
	RAPP	Otolith Technique	0.417	87	0.546	0.0001
		Common Hatch Date	0.377	793	0.418	0.0001
		Modal Progression	0.365	793	0.739	0.0618
	MATT	Otolith Technique	0.597	78	0.433	0.0001
		Common Hatch Date	0.325	241	0.591	0.0001
		Modal Progression	0.483	241	0.814	0.0354
	PAM	Otolith Technique	0.530	72	0.767	0.0001
		Common Hatch Date	0.391	267	0.672	0.0001
		Modal Progression	0.505	267	0.897	0.0428

Table 3.4. Bi-weekly length-frequency modal progression data for the James and Rappahannock Rivers in 1986, and for all river populations in 1987.

COLLECTION DATES	JAMES RIVER		RAPP RIVER	
	MODE	N	MODE	N
1-30 JUNE	19.12	47	16.40	86
1-14 JULY	29.22	29	35.48	116
15-31 JULY	42.69	175	ND	0
1-14 AUGUST	47.65	107	44.95	55
15-31 AUGUST	50.80	148	51.19	35

COLLECTION DATES	JAMES RIVER		RAPP RIVER		MATT RIVER		PAM RIVER	
	MODE	N	MODE	N	MODE	N	MODE	N
1-30 JUNE	16.40	47	19.12	87	19.91	54	21.42	49
1-14 JULY	34.70	39	30.20	308	23.26	80	24.68	74
15-31 JULY	36.48	106	33.36	159	42.98	41	27.65	39
1-14 AUGUST	37.52	104	37.16	135	35.90	30	46.40	81
15-31 AUGUST	42.00	165	38.39	104	37.69	36	37.01	24

variations in birthdates or growth rates among individual fish, as does the otolith aging technique.

The low coefficients of determination of the standard length-age regressions from the otolith aging technique (Table 3.5) and the unreliable growth rate estimates using length-frequency modal progression provide corroborating evidence that length of juvenile striped bass is an unreliable estimate of age of individual fish or population growth rates. Variability in observed standard lengths to estimated age the James River in 1986 was so large that a 60 mm fish could have an estimated age ranging from 40 to 140 days old (Figure 3.9 A). Less extreme but still extensive variability, was found in all other river populations studied (Figures 3.9 A-F).

Estimates of population growth rates in mm/day and g/day were calculated as the slope of the regression of standard length or wet weight on estimated age from the otolith aging technique (Table 3.6). Growth in length in 1986 were 0.301 mm/day in the Rappahannock River to 0.411 mm/day in the James River. Growth in length in 1987 ranged from 0.417 mm/day in the Rappahannock River to 0.597 mm/day in the Mattaponi River. The Rappahannock River had the slowest apparent growth rates in both length and weight in both 1986 and 1987, with the James River having intermediate growth, and the Mattaponi and Pamunkey Rivers having the fastest growth rates in 1987.

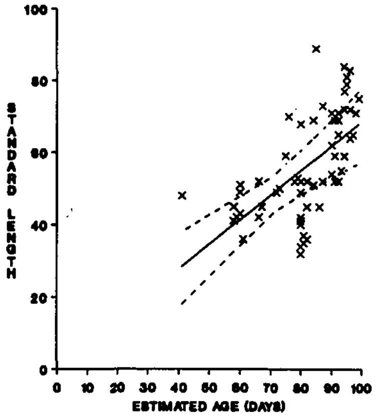
An ANCOVA analysis of growth in length between all rivers in 1986 and 1987 showed no significant difference between

Table 3.5. Juvenile striped bass standard length-estimated age linear regression equations for each separate river population in 1986 and 1987, and for hatchery-reared juvenile striped bass collected in 1987 and 1989 (see Chapter I).

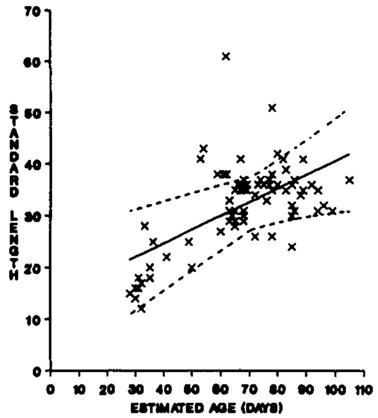
YEAR	RIVER	R-SQ	N	REGRESSION EQUATION
1986	JAMES	0.57	56	SL = 3.62 + 0.411(AGE)
	RAPP	0.52	44	SL = 4.97 + 0.301(AGE)
1987	JAMES	0.76	34	SL = 15.12 + 0.437(AGE)
	RAPP	0.17	74	SL = 14.90 + 0.417(AGE)
	MATT	0.31	49	SL = 8.14 + 0.597(AGE)
	PAM	0.34	76	SL = 7.68 + 0.530(AGE)
1987	HATCHERY	0.57	28	SL = 1.25 + 0.831 (AGE)
1989	HATCHERY	0.84	22	SL = 2.76 + 0.862 (AGE)

Figure 3.9. Regression of standard length on estimated age from the otolith aging technique showing the variability in length-at-age of juvenile striped bass. A: James River 1986, B: Rappahannock River 1986, C: James River 1987, D: Rappahannock River 1987, E: Mattaponi River 1987, and F: Pamunkey River 1987.

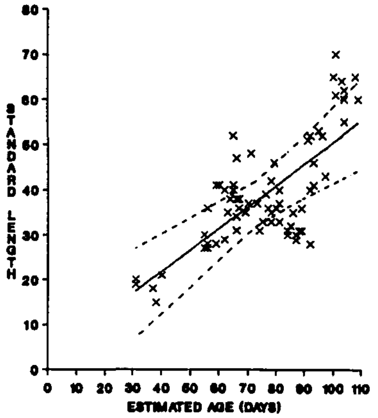
A JAMES RIVER 1986



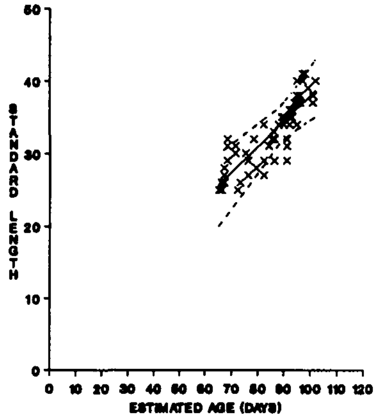
B RAPPAHANNOCK RIVER 1986



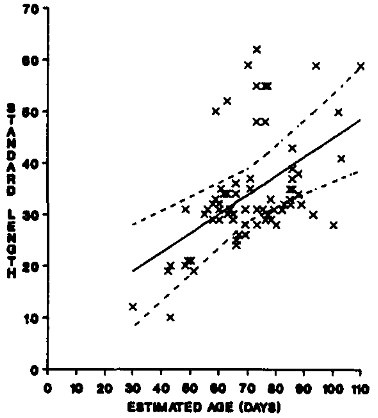
C JAMES RIVER 1987



D RAPPAHANNOCK RIVER 1987



E MATTAPONI RIVER 1987



F PAMUNKEY RIVER 1987

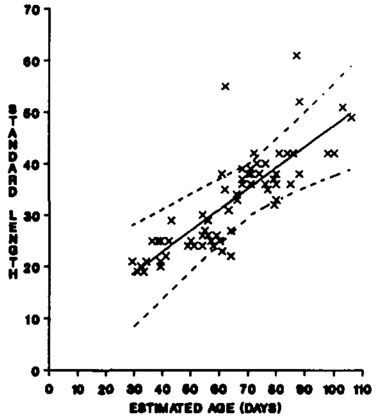


Table 3.6. Growth rates in mm/day and g/day with 95% confidence intervals for all estimates. Estimates for each separate river population were calculated as the slope of the regression of standard length or wet weight on estimated age from the otolith aging technique for the period 1 July-30 August.

YEAR	RIVER	MM/DAY	95% C.I.	G/DAY	95% C.I.
1986	JAMES	0.411	0.302-0.520	0.070	0.046-0.094
	RAPP	0.301	0.245-0.357	0.027	0.024-0.030
1987	JAMES	0.437	0.330-0.544	0.051	0.037-0.065
	RAPP	0.417	0.335-0.499	0.028	0.020-0.036
	MATT	0.597	0.462-0.732	0.124	0.078-0.170
	PAM	0.530	0.460-0.600	0.054	0.042-0.066

slopes (P=0.3375), indicating that growth in length is similar between populations and year-classes. The non-significance of growth in length may be due to the small sample sizes used in this study and the large confidence intervals about the growth rate estimates. Non-overlapping confidence intervals were found between the Rappahannock River in 1986 and the Mattaponi and Pamunkey Rivers in 1987.

Growth rate in weight were 0.027 g/day in the Rappahannock River and 0.070 g/day in the James River in 1986 (Table 3.6). Growth in weight for 1987 ranged from 0.028 g/day in the Rappahannock River to 0.124 g/day in the Mattaponi River. The Rappahannock River had the slowest growth in weight in both years, while the James River had intermediate growth, and the Mattaponi River had the fastest growth in weight. An ANCOVA analysis of growth in weight between rivers in both years showed a significant difference between the Mattaponi River in 1987 and all other rivers (P<0.0001).

Striped bass in the Mattaponi River in both years grew fastest in both length and weight, while those in the Rappahannock River grew slowest. The James River grew at intermediate rates in length and weight, and the Pamunkey River had a fast growth rate in length but only an intermediate growth rate in weight. It appears that on average, growth of juvenile striped bass is similar in both length and weight of the fish. However, significant differences were only apparent for growth in weight in the Mattaponi River.

INDIVIDUAL GROWTH RATES

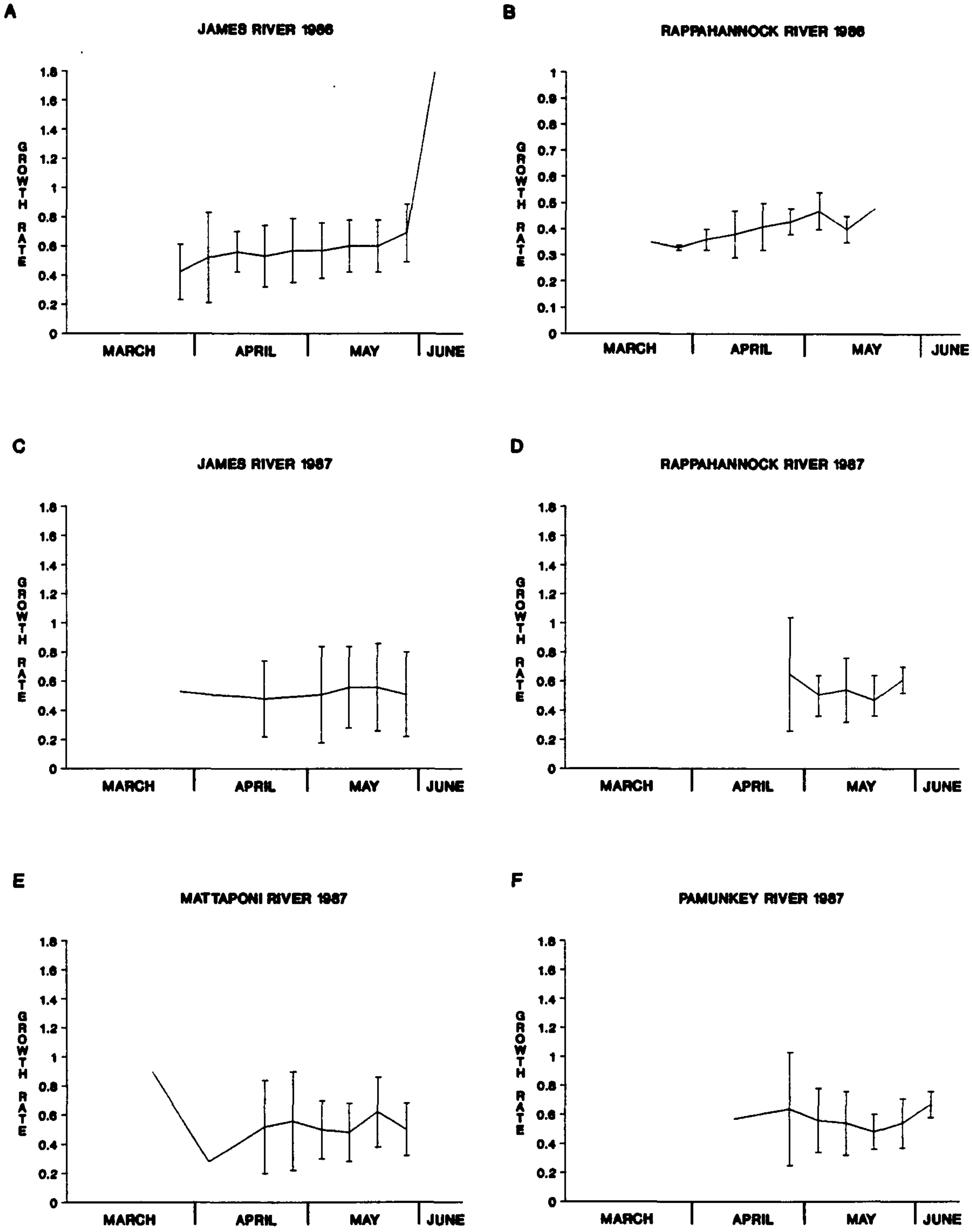
Growth rates of individual fish were calculated from the following formula:

$$GR = (SL - 3.1\text{mm}) / \text{EST. AGE}$$

where GR is growth rate in mm/day, SL is standard length of the fish at time of capture, and 3.1 is the average size at hatch. Mean growth rates +/- 1STD were plotted against weekly birthdate intervals to determine if growth rate differences existed between spawning cohorts (Figures 3.10 A-F).

There was a great deal of overlap in the confidence intervals around the mean growth rate for all cohorts in each river and, therefore, no significant differences were observed. A general increase in growth rates of later produced cohorts spawned in 1986 was observed (Figure 3.10 A and B). In the Rappahannock River in 1986, fish hatched in late March averaged 0.34 mm/day, while fish hatched in May averaged 0.54 mm/day. Growth rates increased more gradually in the James River in 1986 from 0.45 mm/day for the late March cohort to 0.59 mm/day for fish hatched in May. Average growth rates for the early hatched cohort in the Rappahannock River were 25% slower than early hatched fish from the James River.

Figure 3.10. Mean growth rates in mm/day +/- 1 STD, by weekly birthdate cohorts. A: James River 1986, B: Rappahannock River 1986, C: James River 1987, D: Rappahannock River 1987, E: Mattaponi River 1987, and F: Pamunkey River 1987.


A
JAMES RIVER 1986
B
RAPPAHANNOCK RIVER 1986
C
JAMES RIVER 1987
D
RAPPAHANNOCK RIVER 1987
E
MATTAPONI RIVER 1987
F
PAMUNKEY RIVER 1987
GROWTH RATE
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
0.1
0.3
0.5
0.7
0.8
0.9
MARCH
APRIL
MAY
JUNE

However, average growth rates of fish hatched in mid-May were only 8% slower in the Rappahannock River. In 1987 there were again no significant differences between cohort growth rates due to the overlap of 95% confidence intervals. A general comparison of average cohort growth rates, however, showed no increase with season (Figure 3.10 C-F).

Average growth rates were calculated for 1986 and 1987 when all rivers were combined (Table 3.7), however, overlapping confidence intervals again produced non-significant results. These data generally show increasing growth rates with progressing birthdates in 1986 and relatively constant growth rates between cohorts in 1987. Average growth rates of fish hatched between 8-14 April and 15-21 April were 16.4 and 11.8% faster in 1987 than in 1986, respectively. The 22-30 April cohort had an average growth rate 3.8% faster in 1987. Fish hatched between 1-14 May had similar growth rates in both years, with the 1986 cohorts growing approximately 2% faster than the 1987 cohorts. The 15-21 May and 22-31 May cohorts grew 9.3 and 26.8% faster in 1986, respectively. The discrepancy between average growth rates for weekly cohorts in 1986 and 1987 may be due to variations in the relative sizes of cohorts between year-classes, with larger relative sizes in the month of April in 1986 and the month of May in 1987. Generally, the period of larger cohort sizes in both years corresponded to the period

Table 3.7. Average growth rates in mm/day for pooled rivers systems in 1986 and 1987 for weekly birthdate cohorts. Growth rates were calculated from the equation GR = (SL - 3.1mm)/AGE, where GR = growth rate in mm/day, SL = standard length, and AGE = the estimated age of each individual fish from the otolith aging technique.

BIRTHDATE	1986 (MM/DAY)	1987 (MM/DAY)
22-31 MARCH	0.38	----
1-7 APRIL	0.41	----
8-14 APRIL	0.46	0.55
15-21 APRIL	0.45	0.51
22-30 APRIL	0.51	0.53
1-7 MAY	0.54	0.53
8-14 MAY	0.55	0.54
15-21 MAY	0.59	0.54
22-31 MAY	0.71	0.56

of slower growth, even though the results were not significant.

MORTALITY ESTIMATES

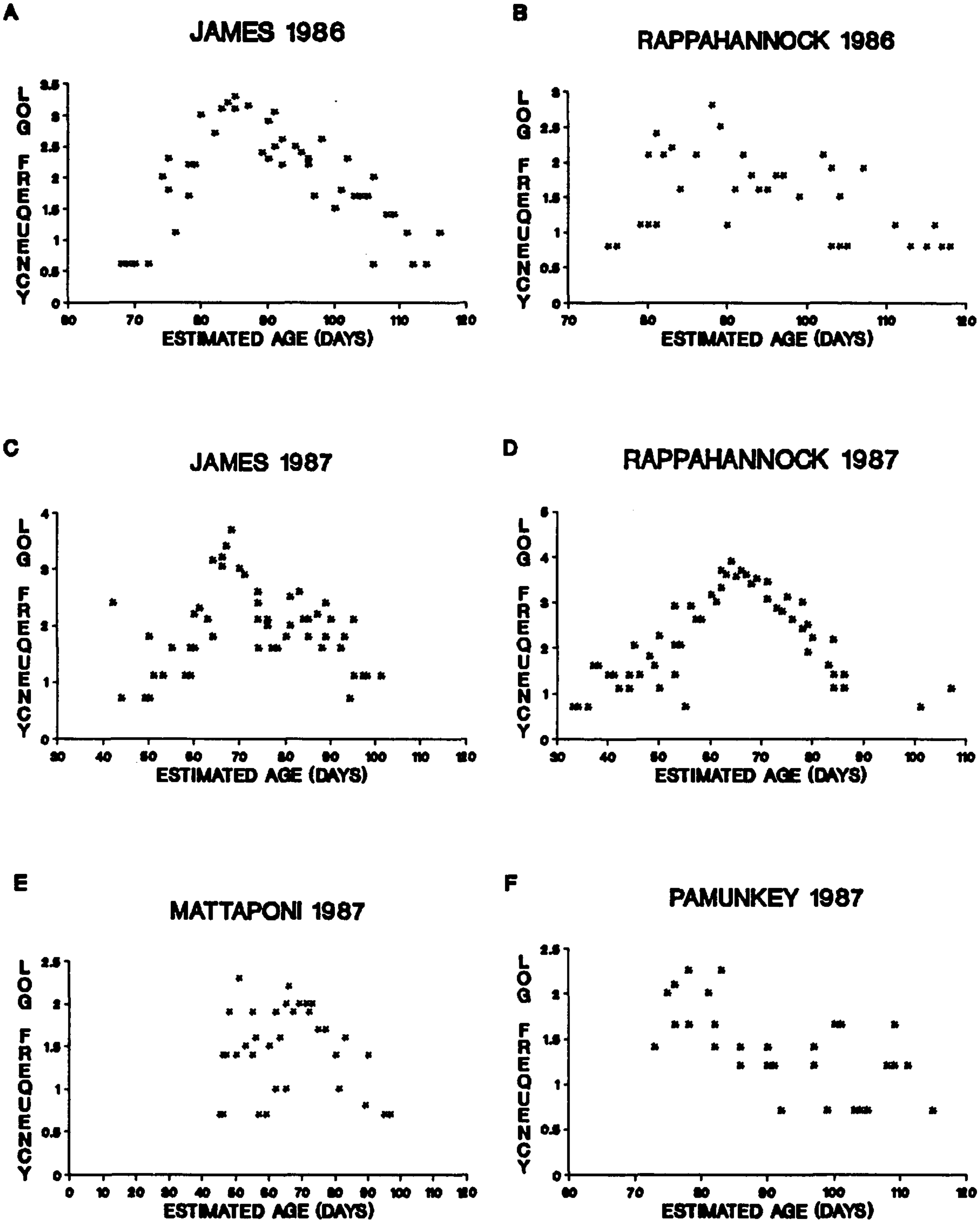
Age-standard length regressions for each separate river population were calculated from the subsample of aged fish in each population (Table 3.8). The Pamunkey and Mattaponi Rivers in 1986 were not included in this analysis due to small sample sizes. Coefficients of determination ranged from 0.348 in the James River in 1986 to 0.767 in the Pamunkey River in 1987, showing a great deal of variability in this relationship.

Daily instantaneous mortality was estimated from the negative slope of the descending limb of the catch curves for each population studied (Figure 3.11 A-F). The catch curve for the James River in 1986 (Figure 3.11 A) shows that fish did not fully recruit to the gear until reaching approximately 80 days old, estimated from the dome of the catch curve. Therefore, the descending limb was truncated at a lower limit of 80 days in this river. Fish in all other rivers appeared to recruit to the sampling gear by approximately 65 days of age, but were not equally vulnerable to the gear at ages greater than 90 days. The descending limb for all other rivers was truncated at a lower limit of 65 days. An upper limit of 90 days was applied to all rivers due to the apparent gear selectivity at older ages.

Table 3.8. **Estimated age-standard length regressions for each separate river population in 1986 and 1987.**

YEAR	RIVER	N	R-SQ	REGRESSION EQUATION
1986	JAMES	113	0.348	AGE = 43.02 + 0.847(SL)
	RAPP	83	0.588	AGE = 11.16 + 1.951(SL)
1987	JAMES	82	0.451	AGE = 29.73 + 1.033(SL)
	RAPP	87	0.544	AGE = 18.22 + 1.305(SL)
	MATT	77	0.433	AGE = 34.43 + 0.931(SL)
	PAM	72	0.767	AGE = 12.17 + 1.447(SL)

Figure 3.11. Catch curves from plots of log frequency on estimated age from the otolith aging technique. A: James River 1986, B: Rappahannock River 1986, C: James River 1987, D: Rappahannock River 1987, E: Mattaponi River 1987, and F: Pamunkey River 1987.


A
JAMES 1986
LOG FREQUENCY
0
0.5
1
1.5
2
2.5
3
3.5
60
70
80
90
100
110
120
ESTIMATED AGE (DAYS)
B
RAPPAHANNOCK 1986
LOG FREQUENCY
0
0.5
1
1.5
2
2.5
3
70
80
90
100
110
120
ESTIMATED AGE (DAYS)
C
JAMES 1987
LOG FREQUENCY
0
1
2
3
4
30
40
50
60
70
80
90
100
110
120
ESTIMATED AGE (DAYS)
D
RAPPAHANNOCK 1987
LOG FREQUENCY
0
1
2
3
4
5
30
40
50
60
70
80
90
100
110
ESTIMATED AGE (DAYS)
E
MATTAPONI 1987
LOG FREQUENCY
0
0.5
1
1.5
2
2.5
0
10
20
30
40
50
60
70
80
90
100
110
120
ESTIMATED AGE (DAYS)
F
PAMUNKEY 1987
LOG FREQUENCY
0
0.5
1
1.5
2
2.5
60
70
80
90
100
110
120
ESTIMATED AGE (DAYS)

The major assumption of any catch curve analysis is that there is no immigration/emigration and constant recruitment within the populations. To assess this assumption, length frequency plots by 2-week sampling periods were examined for each river population (Appendix B). Sample sizes were too small to perform this analysis for the Pamunkey River in 1987. There appears to be a slight downstream movement of larger striped bass (>60 mm standard length) in the James River in 1986 by the end of August. In all other rivers, there is no apparent immigration or emigration.

Due to variations in time intervals caused by truncating the descending limb of the catch curves, percent loss per day was calculated for each river and then daily instantaneous mortality was recalculated to make all estimates comparable. Percent loss per day ranged from a low value of 1.88% in the Pamunkey River in 1987 to 3.98% in the Rappahannock River in 1987 (Table 3.9). Percent loss/day for the remaining rivers were intermediate between these values.

To determine the effect of variability in the age-length regressions on an estimate of mean mortality, mortality estimates were recalculated with incorporation of the 95% confidence intervals about the predicted age. The ranges of mortality estimates were then compared to determine the reliability of a mean mortality estimate (Table 3.9). There is little or no change in the range of mortality estimates

Table 3.9. Mean mortality estimates in % loss/day and 95% confidence intervals about the estimates for each separate river system in 1986 and 1987, and 95% confidence intervals about the mean mortality estimate when the 95% confidence intervals about the estimated age were included in the analysis.

YEAR	RIVER	MEAN % LOSS/DAY	95% MEAN C.I.	95% C.I. W/ C.I. ABOUT AGE
1986	JAMES	2.81	2.65 - 2.91	2.46 - 2.96
	RAPP	2.48	0.62 - 3.36	0.62 - 3.36
1987	JAMES	2.60	2.56 - 2.63	2.56 - 2.63
	RAPP	3.98	3.88 - 4.04	3.88 - 4.07
	MATT	2.55	1.95 - 2.86	1.41 - 2.86
	PAM	1.88	1.54 - 2.05	0.90 - 2.05

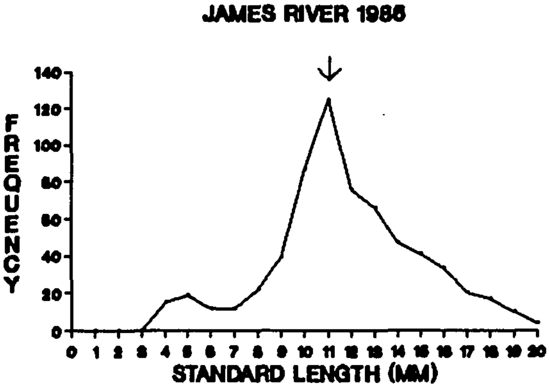
for the James and Rappahannock Rivers in both years, however, there was a large expansion in the lower limit of the estimates for the Mattaponi and Pamunkey Rivers in 1987.

The expansion in the range of mortality estimates does not appear to be related to the variability in the age-length regressions. For example, the Pamunkey River in 1987 had the best fit between age and standard length with a coefficient of determination of 0.77 (Table 3.8), however, there was still an expansion of the range of mortality estimates with incorporation of the 95% confidence intervals about each predicted age. The James River in 1986 had the lowest coefficient of determination at 0.35 (Table 3.8), but little expansion of the range of mortality estimates. The range of mortality estimates, both mean values and those with incorporation of confidence intervals of the age-length regressions, are relatively narrow for all rivers, except the Rappahannock River in 1987, which had a range from 0.62%-3.36% loss/day.

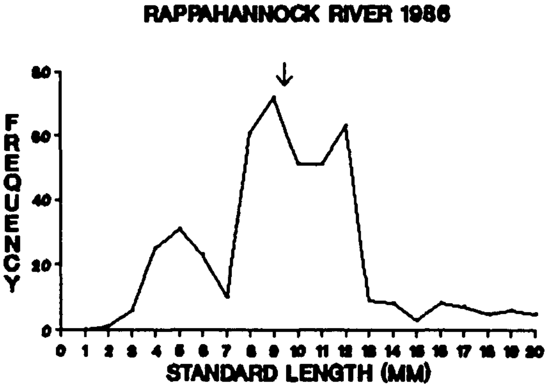
The large range in mortality values for the Rappahannock River in 1987 as well as the shift in ranges with inclusion of the age-length confidence intervals appears to be due to variations in the length frequency distributions of all fish collected in each river (Figures 3.12 A-F). Standard lengths were blocked by 5 mm intervals and frequency plots were constructed. The arrow on all plots indicates the mean length from the age-length regressions. Prediction of age from the

Figure 3.12. Length frequency plots by 5 mm standard length intervals. Arrow marks the mean standard length. A: James River 1986, B: Rappahannock River 1986, C: James River 1987, D: Rappahannock River 1987, E: Mattaponi River 1987, and F: Pamunkey River 1987.

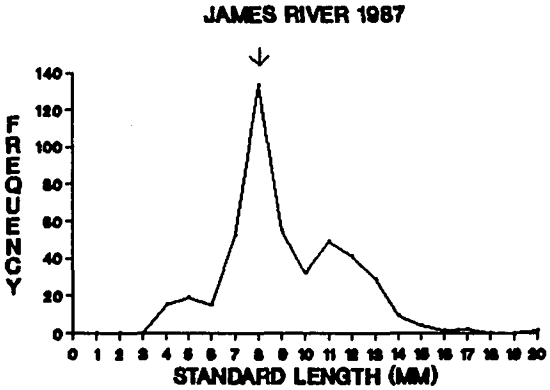
A


JAMES RIVER 1986
FREQUENCY
0
20
40
60
80
100
120
140
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

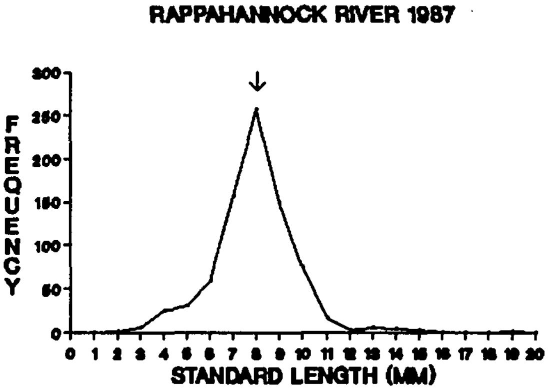
B


RAPPAHANNOCK RIVER 1986
FREQUENCY
0
20
40
60
80
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

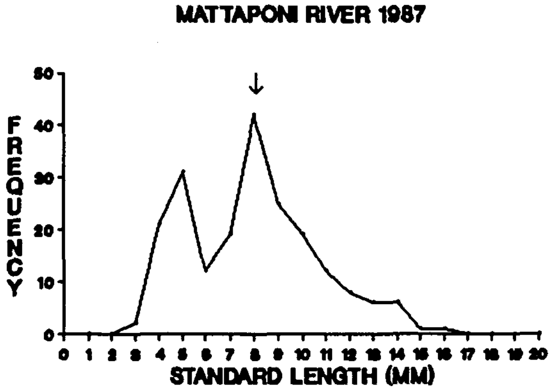
C


JAMES RIVER 1987
FREQUENCY
0
20
40
60
80
100
120
140
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

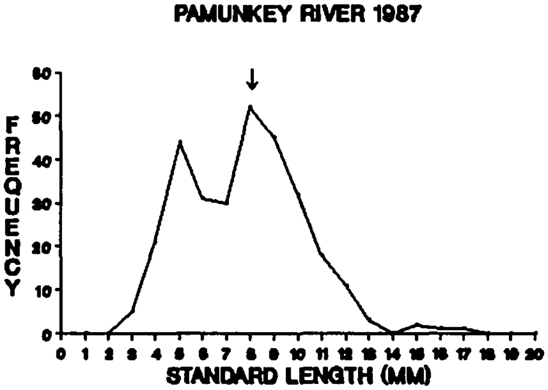
D


RAPPAHANNOCK RIVER 1987
FREQUENCY
0
50
100
150
200
250
300
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

E


MATTAPONI RIVER 1987
FREQUENCY
0
10
20
30
40
50
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

F


PAMUNKEY RIVER 1987
FREQUENCY
0
10
20
30
40
50
60
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
STANDARD LENGTH (MM)

regression will be most reliable near the mean length and less reliable as you progress away from the mean. Therefore, the distribution of lengths about the mean length appears to play an important role in the reliability of mortality estimates calculated with this method.

The large range in mortality estimates in the Rappahannock River in 1986 appears to be caused by the increased dispersion in lengths, as seen from the length frequency distribution for this river (Figure 3.12 B). The James River in 1986, and the James and Rappahannock Rivers in 1987, all had narrow confidence intervals about mean mortality estimates and little or no expansion of the range of values with incorporation of the confidence intervals of the age-length regressions. This appears to be caused by the majority of fish in each river having lengths near the mean standard length (Figures 3.12 A and C-D), thereby giving more reliable predictions of age. The Mattaponi and Pamunkey Rivers in 1987 both showed an expansion of the lower confidence limit about the mortality estimate when the 95% confidence intervals about the predicted age were included in the analysis. The length frequency distributions (Figures 3.12 E-F) for both rivers show a peak at the mean length of approximately 40 mm, and a second peak near 20 mm. Age predictions for fish in this second peak were less reliable than predictions near the mean length, and possibly caused the slope of the descending limb to change, thereby extending the lower limit of mortality estimates for these rivers.

To determine if there were differences in mortality caused by variations in hatching times, percent loss/day was calculated for 14-day cohorts based on the back-calculated birthdate distributions (Table 3.10). Mortality estimates for the majority of cohorts in each river were significantly higher than the overall estimate for the river populations, which are shown in parentheses. Percent loss/day ranged from 3.07% to as high as 9.39%. There were no apparent trends when comparing the estimates for the separate cohorts. For example, the Mattaponi River in 1987 showed higher mortality for the early cohort (fish hatched at the end of April), while the James River in 1987 had much higher mortality for fish hatched later in the season. No apparent relationship was found between mortality and growth rates in mm/day between the early and late spawning cohorts in any of the rivers (Table 3.10).

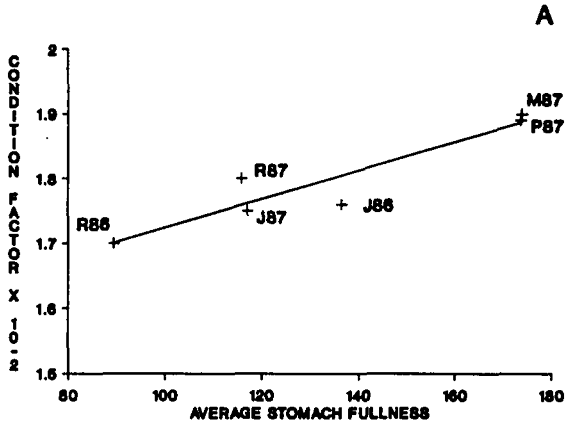
COMPARISON OF GROWTH, MORTALITY, AND ABUNDANCE

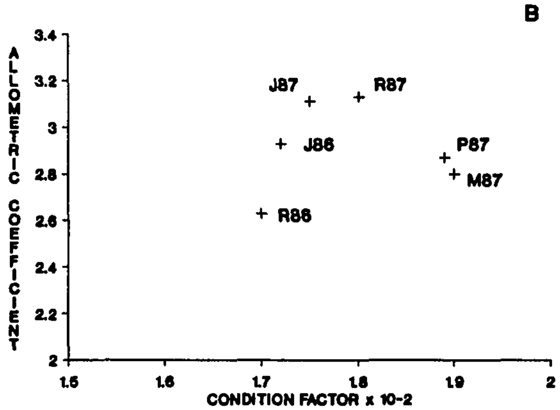
A significant positive linear relationship was found between average condition factor and average stomach fullness (Table 3.1, Figure 3.13 A). No relationship was found between the allometric coefficient and either of these two factors (Figure 3.13 B-C). It appears that the allometric coefficient

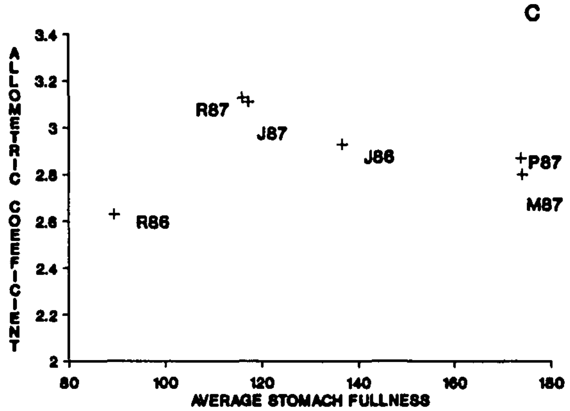
Table 3.10. Comparison of mean growth rates in mm/day, mean daily instantaneous mortality estimates, and % loss/day for 14-day birthdate cohorts. (Early = 1 April-14 April, Mid = 15 April-31 April, and Late = 1 May-14 May). Shown in parentheses are the mean mortality estimates for each river population when all cohorts are combined.

YEAR	RIVER	COHORT	GROWTH RATE (MM/DAY)	Z	% LOSS/ DAY
1986	JAMES	EARLY	0.55	0.215	8.75
	(2.81)	MID	----	-----	----
		LATE	----	-----	----
1987	JAMES	EARLY	0.51	0.163	7.93
	(2.60)	MID	0.56	0.266	6.95
		LATE	0.54	0.289	9.39
	RAPP	EARLY	0.53	0.087	4.78
	(3.98)	MID	0.52	0.087	3.07
		LATE	0.54	0.195	4.88
	MATT	EARLY	0.53	0.220	8.81
	(2.55)	MID	0.52	0.156	7.36
		LATE	0.57	0.100	4.58
	PAM	EARLY	0.65	-----	----
	(1.88)	MID	0.51	0.186	4.86
		LATE	0.51	0.062	4.06

Figure 3.13. Relationships between A: Average annual condition factor and average annual stomach fullness (condition factor = 0.015 + 2.2 * 10-5 (stomach fullness), R-square=0.88, P=0.006), B: average annual condition factor and the population allometric coefficient, and C: average annual stomach fullness and the population allometric coefficient.


A
CONDITION FACTOR X 10-2
2
1.9
1.8
1.7
1.6
1.5
80
100
120
140
160
180
AVERAGE STOMACH FULLNESS
M87
P87
R87
J87
J86
R86


B
ALLOMETRIC COEFFICIENT
3.4
3.2
3
2.8
2.6
2.4
2.2
2
1.5
1.6
1.7
1.8
1.9
2
CONDITION FACTOR x 10-2
J87
R87
J86
P87
M87
R86


C
ALLOMETRIC COEFFICIENT
3.4
3.2
3
2.8
2.6
2.4
2.2
2
80
100
120
140
160
180
AVERAGE STOMACH FULLNESS
R87
J87
J86
P87
M87
R86

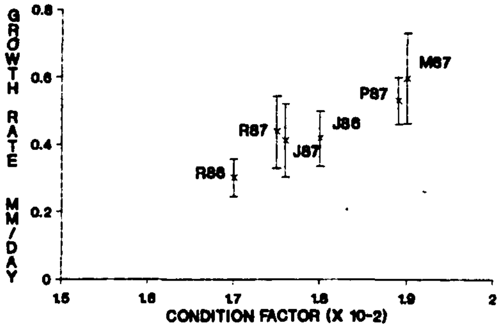
from length-weight data may not be a reliable means of assessing the robustness of individual juvenile striped bass. The relationship between condition factor and allometric coefficient may have been obscured by the use of the allometric coefficient to calculate condition factor. Condition factor was used to evaluate the relationship between growth, mortality, abundance, and robustness of fish in each population.

The relationship between growth in mm/day and average annual condition factor was linear (P=0.005) and had a coefficient of determination of 0.89 (Figure 3.14 A). The relationship between growth in g/day had a coefficient of determination of 0.41 (Figure 3.14 B), but was not significant (P=0.171). No apparent relationship was found between mortality and condition factor (Figure 3.14 C). However, on average it appears that populations with faster growth rates and lower mortality rates consist of fish in better condition.

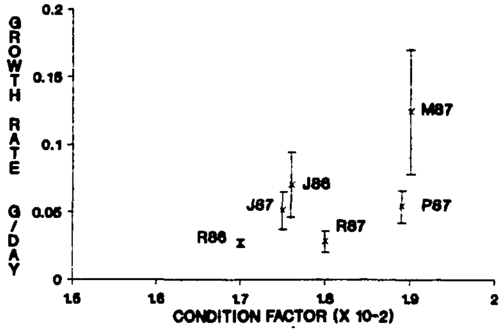
No relationship was found between daily instantaneous mortality and either growth in mm/day or g/day (Figures 3.15 A and B). The least-squares linear regression produced non-significant regression of mortality on growth rates (P=0.6120 for growth in mm/day and P=0.5770 for growth in g/day). Confidence intervals overlapped for all rivers except the Rappahannock River in 1987 which had a slow growth rate in both length and weight, and higher mortality than all other rivers. The confidence intervals for the Rappahannock River

Figure 3.14. Relationships between A: Population growth rates in mm/day and avenge annual condition factor, (growth rate = -1.73 + 121.15 (condition factor), R-square=0.89, P=0.005), B: Population growth rates in g/day and average annual condition factor, and C: Daily instantaneous mortality and average annual condition factor.

A


GROWTH RATE MM/DAY
0.8
0.6
0.4
0.2
0
1.5
1.6
1.7
1.8
1.9
2
CONDITION FACTOR (X 10-2)
R86
R87
J87
J86
P87
M87

B


GROWTH RATE G/DAY
0.2
0.15
0.1
0.05
0
1.5
1.6
1.7
1.8
1.9
2
CONDITION FACTOR (X 10-2)
R86
J87
J86
R87
M87
P87

C

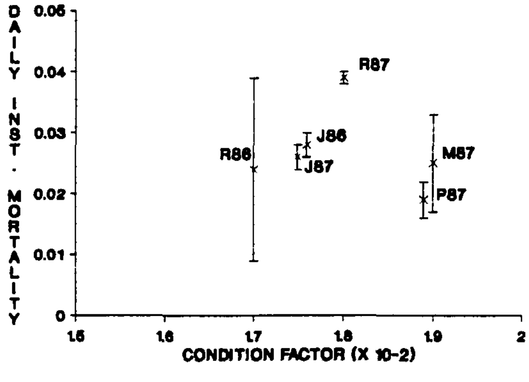
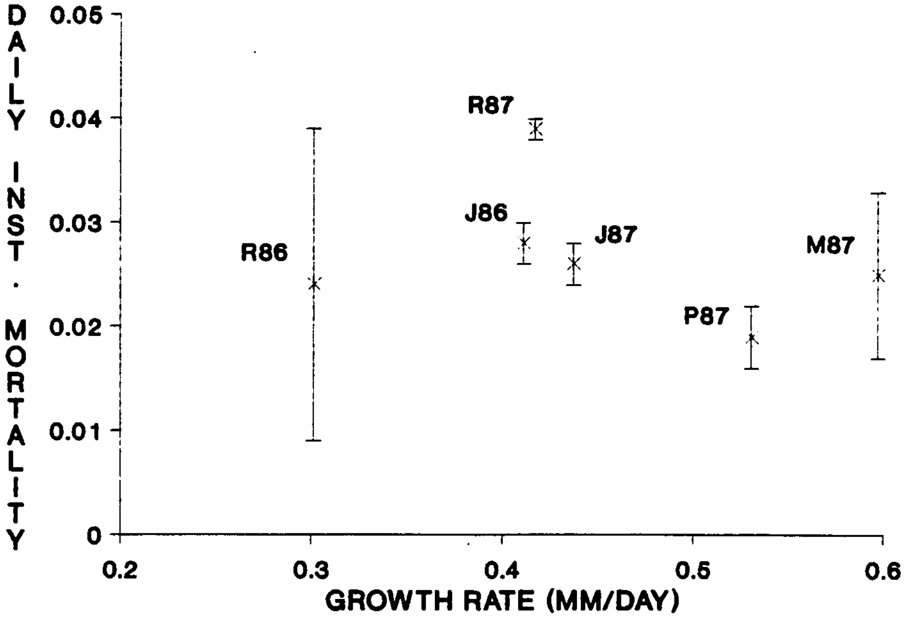
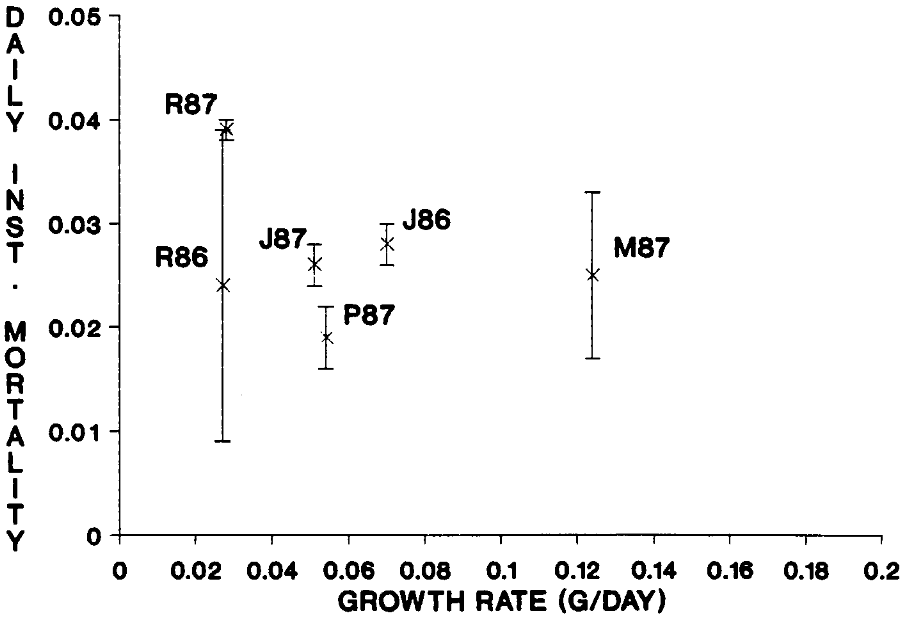

DAILY INST. MORTALITY
0.05
0.04
0.03
0.02
0.01
0
1.5
1.6
1.7
1.8
1.9
2
CONDITION FACTOR (X 10-2)
R87
J86
R86
J87
M87
P87

Figure 3.15. Relationships between A: Daily instantaneous mortality and population growth rates in mm/day, and B: Daily instantaneous mortality and population growth rates in g/day.

A


DAILY INST. MORTALITY
0.05
0.04
0.03
0.02
0.01
0
0.2
0.3
0.4
0.5
0.6
GROWTH RATE (MM/DAY)
R87
J86
J87
R86
M87
P87

B

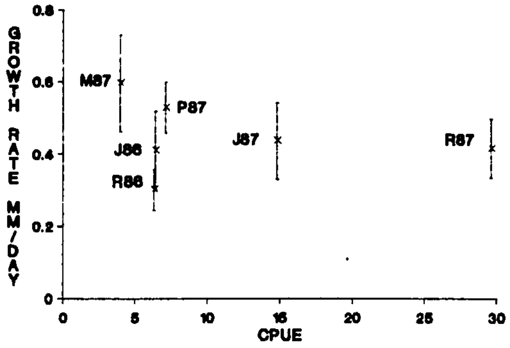

DAILY INST. MORTALITY
0.05
0.04
0.03
0.02
0.01
0
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
0.16
0.18
0.2
GROWTH RATE (G/DAY)
R87
J86
J87
R86
P87
M87

in 1986 were extremely large compared to all other rivers, and overlapped all rivers except the Rappahannock River in 1987. This population had much slower growth in length then all other rivers, but comparable growth in weight to the Rappahannock River in 1987, but lower than all other rivers. The deletion of the Rappahannock River in 1986 from the least-squares linear regression analysis for growth in length does not improve the relationship (P=0.5346).

No apparent relationship was found between growth in length or weight and catch-per-unit-effort, as measured as the number of fish caught per seine haul (Figure 3.16 A and B). The Mattaponi River in 1987 had the lowest CPUE at 4 fish/haul and the fastest growth at almost 0.6 mm/day and 0.12 g/day. The James and Rappahannock Rivers in 1986 and the Pamunkey River in 1987 all had intermediate CPUE values, ranging from 6-7 fish/haul. Growth rates for these rivers were variable, ranging from 0.3-0.5 mm/day and 0.03-0.07 g/day, with no trends being apparent. Growth rates in mm/day for the James and Rappahannock Rivers in 1987 were approximately 0.4 mm/day, while CPUE ranged from 15-30 fish/haul. Growth rates tended to decrease at higher CPUE values. For example, the James River in 1987 had intermediate growth at 0.05 g/day and an intermediate CPUE at 15 fish/haul, while the Rappahannock River in 1987 had slower growth at 0.03 g/day and a much higher CPUE at close to 30 fish/haul.

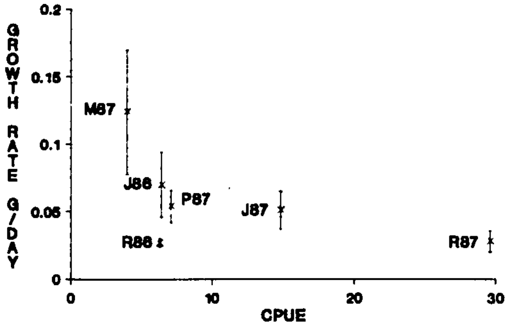
Figure 3.16. Relationships between A: Population growth rates in mm/day and average annual catch-per-unit-effort, as an index of relative abundance, B: Population growth rates in g/day and average annual catch-per-unit-effort, and C: Daily instantaneous mortality and average annual catch-per-unit-effort (mortality = 0.02 + 5.9 * 10-4 (CPUE), R-square=0.72, P=0.032).

A



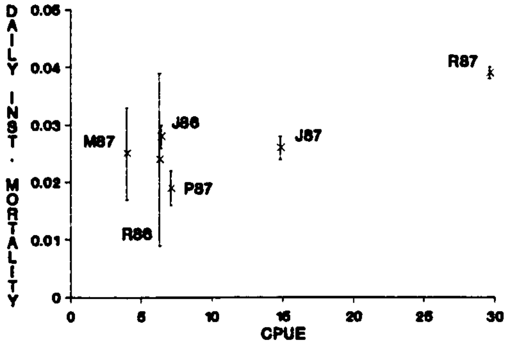
GROWTH RATE MM/DAY
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
CPUE
M87
P87
J86
R86
J87
R87

B



GROWTH RATE G/DAY
0.2
0.15
0.1
0.05
0
0
10
20
30
CPUE
M87
J86
P87
J87
R86
R87

C



DAILY INST. MORTALITY
0.05
0.04
0.03
0.02
0.01
0
0
5
10
15
20
25
30
CPUE
R87
J86
M87
J87
P87
R86

A significant linear relationship (P=0.032) was found between daily instantaneous mortality and CPUE, with coefficient of determination of 0.72 (Figure 3.16 C). Daily instantaneous mortality estimates increased with increasing CPUE. Overlap of 95% confidence intervals occurred at low and intermediate CPUE values, with mortality estimates ranging from 0.17-0.28 (J86, R86, J87, M87, and P87). In the Rappahannock River in 1987, CPUE increased to close to 30 fish/haul and mortality increased to approximately 0.04, showing no overlap in the 95% confidence intervals with any of the other rivers. The Rappahannock River in 1987 appears to be an influential observation that drives the significant relation between daily instantaneous mortality and CPUE. In the absence of this data point there is no apparent relationship between these factors.

DISCUSSION

Juvenile striped bass were collected in shallow inshore waters at salinities of 0-12.2 ppt and temperatures ranging from 23.0-33.5 C, with the majority of fish collected in brackish waters (0-5 ppt) and temperatures greater than 26 C. The range of temperatures in which juvenile striped bass were collected corresponds well with the average optimum growth temperatures of 24-30 C obtained by Coutant et al. (1984), Cox and Coutant (1981), and Kellog and Gift (1983). Cech et al. (1984) found fastest growth at 25 C and highest mortality at temperatures less than 20 C. Otwell and Merriner (1975) found that mean relative growth rate (fork length attained expressed as a percentage of the initial fish length) decreased from 20.0-1.0% as temperature decreased from 24-12 C, and found fastest growth at intermediate salinities. They concluded from their studies that temperature was more limiting to striped bass growth and survival than was the effect of salinity. The ranges of temperatures and salinities in 1986 and 1987 in Virginia nursery areas appears to be consistent with maximum growth and survival of juvenile striped bass. Growth and survival appeared to be related to the extension of the range in distribution into less saline waters in 1987, as seen from the high level of abundance in that year.

A comparison of the back-calculated birthdate distributions showed consistency between rivers within years, but not between years. In both the James and Rappahannock Rivers in 1986, birthdates had modes occurring in the last week of April and the first week of May. The 1987 birthdate distributions were skewed to late in the season with a mode occurring in the second week of May in all rivers. The range of birthdates (March-June) corresponds with the time of spawning known to occur in the Chesapeake Bay (Chapoton and Sykes 1961; Dovel 1971; Kernehan et al. 1981; and Setzler-Hamilton 1981). Egg and larval studies were not conducted in these years in Virginia tributaries, therefore, patterns of survival from the egg to the juvenile stage could not be examined.

Back-calculated birthdate distributions were used to compare growth and mortality of fish hatched early and late in the season. On average, growth rates of weekly cohorts increased with progression of the season in 1986, but remained relatively constant in 1987; differences, however, were not significantly different due to overlapping confidence intervals. A general comparison of average growth rates for each year-class when all rivers were combined showed faster growth for April cohorts in 1987 and for May cohorts in 1986. The variations in cohort growth rates between year-classes appear to be related to relative cohort size of fish surviving to the juvenile stage. The peak in the birthdate distributions occurred in late April-early May in 1986 and in mid-May in 1987. A density-dependent effect, in the form of increased competition for either food or space, may have caused lowered growth rates of the larger cohorts. This method of growth rate calculation estimates average growth rates from hatching until capture. Therefore, the estimated growth rates between cohorts may be influenced by the length of time the fish have had to grow.

The comparison of mortality estimates for 14-day cohorts did not show any trends between early and late hatched fish, and showed no relationship to average growth rates calculated for the same time periods. Houde et al. (1990) found that cohort-specific growth and mortality tended to increase with season in Potomac River larval striped bass in 1987, but not in 1988. They also found no significant relationship between cohort-specific mortality and instantaneous growth rates in either year. Crecco and Savoy (1985) also found increasing age-specific growth rates of American shad larva with season, but found no such trends in juvenile growth rates.

The slower growth rates of earlier hatched fish may be a function of the suboptimal temperature regime experienced by these fish. Houde et al. (1990) found a positive relationship between mean water temperature in the first 20 days post-hatch and the cohort's Julian date of birth, which indicates that conditions for larval survival generally improved during the 1987 spawning season in the Potomac River Estuary. Uphoff (1989), using length-based age estimates, found a significant correlation between mean water temperature and growth of striped bass larvae in the Choptank River from 1980-1985. Dey (1981) found a similar correlation between growth and mean water temperature in Hudson River striped bass populations in 1975-1976. Dey (1981) also suggested that a sudden decrease in water temperature in the Hudson River Estuary during late May 1976 caused high mortality of larvae spawned before that date. Cech et al. (1984) calculated specific growth rates using the change in initial and final live body weight with time. They found that striped bass growth benefited from the warmest experimental conditions (25 C), and all mortalities occurred at 15 and 20 C. Redpath (1972) concluded that the optimum temperature for juvenile striped bass was near 16 C. Poor growth was found at 12 C due to higher maintenance requirements, which left less energy available for growth. Koo and Ritchie (1973) found that when water temperatures dropped below 10 C, striped bass growth and feeding activity ceased.

A comparison of growth rate estimates from the three methods provided similar results between the otolith aging technique and the use of a common hatch date. The slight differences in estimates made by these methods may be due to the use of a common hatch date not based on observed spawning frequency. The use of length-frequency modal progression appears to be an unreliable method of estimating growth of juvenile striped bass. Growth rates were higher in 1986 and lower in all rivers in 1987, as compared to the other two techniques. The low coefficients of determination of the age-standard length regressions and the unreliable growth rate estimates using length-frequency modal progression provide evidence that length of young-of-the-year striped bass is not a reliable indicator of age.

Growth rate estimates from the otolith aging technique ranged from 0.301-0.597 mm/day and 0.027-0.124 g/day. No significant differences were found between rivers or year-classes when comparing growth in length, however, the Mattaponi River in 1987 had significantly faster growth in weight than all other rivers. The ranking of growth rates in both length and weight was similar between years, with the Rappahannock River having slowest growth, the James River having intermediate growth, and fish from the Mattaponi and Pamunkey Rivers having fastest growth rates. Secor et al. (1989), also using the otolith aging technique, reported faster growth rates for young-of-the-year striped bass from Santee-Cooper, South Carolina. Growth rates were 0.1 mm/day in 1986 and 1.1 mm/day in 1987 for striped bass collected in June and July. Trent (1962) observed growth rates from 0.272-0.433 mm/day in Albemarle Sound, North Carolina for fish collected between June-September. Rathjen and Miller (1957) collected striped bass from June-October and calculated an average growth rate of 0.45 mm/day for Hudson River striped bass. Dey (1981) reported higher growth rates for young-of-the-year striped bass in the Hudson River at 0.8 mm/day from mid-June to mid-August. The faster growth rates found by Secor et al. (1989) and Dey (1981) may have been due to sampling of juvenile striped bass earlier in the season when fish were growing at a faster rate. This may be an indication that striped bass growth rates are not linear prior to the juvenile stage.

Mortality estimates for 60-90 day old striped bass calculated from an age-based catch curve analysis ranged from 1.88% loss per day in the Pamunkey River in 1987 to 3.98% loss per day in the Rappahannock River in 1987. Essig and Cole (1986) determined the reliability of this method for estimating mortality of larval alewives through a comparison to the decline in catch-per-unit-effort. A comparison could not be performed for young-of-the-year striped bass since the decline in CPUE did not produce significant regressions. Houde et al. (1990) calculated cohort-specific mortality estimates for Potomac River larval striped bass in 1987. Mortality was estimated at 7-32% loss/day, which is slightly higher than estimates for juvenile striped bass, as would be expected. Uphoff (1989) calculated daily mortality of early juvenile striped bass in the Choptank River at 2-4% loss/day.

Dey (1981) estimated daily instantaneous mortality for early juvenile striped bass in the Hudson River in 1975 and 1976 at 5% loss/day, and 0.5% loss/day for juveniles in mid-summer. Turner and Chadwick (1972) and Polgar (1977) estimated mortality for postfin-fold larvae at 3.0-7.7% loss/day and 7-12% loss/day, respectively. The estimates of daily instantaneous mortality in the present study (1.88-3.98% loss/day) are lower than the estimates of Turner and Chadwick (1972) and Polgar (1977), which would be expected for older fish. However, the present estimates are much higher than those of Dey (1981) for striped bass greater than 50 mm in length. Dey (1981) suggested that his estimates may have been biased by gear avoidance and dispersal from the sampling area. The estimates in the present study were calculated from an age-based catch curve analysis, while the estimates of Dey (1981) were based on the estimated standing crop of juvenile striped bass in the Hudson River, and those of Uphoff (1989) were based on age estimates from lengths of striped bass larvae. Estimates based on specific ages of individual fish appear to be more reliable than the methods employed by Dey (1981) and Uphoff (1989) for young-of-the-year striped bass.

The age-standard length regressions calculated from a subsample of fish in each population showed low coefficients of determination, again providing evidence of a poor relationship between age and length of juvenile striped bass. This lack of fit on an individual basis, however, did not appear to affect the calculation of a mean population mortality estimate for juvenile striped bass as long as the mean length corresponds to the peak in the length-frequency distributions.

Mortality estimates may have been affected by an incorrect assumption of no immigration/emigration or non-constant recruitment within each population. Raney (1952), Markle and Grant (1970), and Kernehan et al. (1981) found evidence of movement of young-of-the-year striped bass downstream and shoreward during their first summer. Ritchie and Koo (1968) and Setzler-Hamilton et al. (1981) found some upstream movement of juvenile striped bass in the Patuxent and Potomac Rivers, respectively. Comparisons of length frequency plots between upper and lower stations within each river for 2-week periods showed no significant trends in the majority of rivers, indicating that fish were not migrating up- or downriver in any consistent fashion. The slight emigration possibly occurring in the James River in 1986 did not occur until the end of August. Therefore, it was felt that the assumption of no immigration or emigration was correct, at least for the period of time included in this analysis (June-August). Evidence was provided through the calculation of population catch curves that larger, older striped bass were not fully recruited to the sampling gear, which may have been caused by emigration. However, for the majority of these analyses, the larger, older striped bass were truncated out.

Abundance of young-of-the-year striped bass was measured as the number of fish per seine haul. CPUE ranged from 4.0 in the Mattaponi River in 1987 to 29.6 in the Rappahannock River in 1987. Abundance was above average in 1986 with values close to 6.5 fish/haul and extremely high in the James and Rappahannock Rivers in 1987. Trent (1962) suggested that higher abundances occurred in years when the peak spawning date was close to mid-May. In the present study, higher abundances were found in 1987 when the peak of the back-calculated birthdate distributions was in mid-May. It may be possible that a match between spawning and environmental conditions occurring in May can lead to increased survival of striped bass, thereby producing a larger year-class.

Growth rates in mm/day and g/day were positively related to condition factor and average stomach fullness, however, only the relationship between growth in length and condition factor/stomach fullness was significant. The relationship between growth and average stomach fullness (and condition factor) suggests that growth rates of juvenile striped bass may be controlled by the availability of prey items. Trent (1962) found no relationship between growth rate and condition factor; however, he derived condition factors as a ratio of final weight to initial weight, and not of weight and length as in the present study. Dey (1981), upon finding no significant correlations between instantaneous growth rates of Hudson River juvenile striped bass and mean water temperature or mean freshwater flow, suggested that food availability may play a more important role in regulating juvenile striped bass growth. Cooper (1953) and Kramer and Smith (1960) found a relationship between growth rate and condition factor for brown trout and largemouth bass, respectively. They also suggested that food availability may be the most influential factor controlling the growth of these fishes. Suthers et al. (1989) found a relationship between recent growth of larval cod, measured from otolith increment widths, and prey abundance and quality. Karakiri et al. (1989) also suggested that food limitation was responsible for growth differences of plaice between years. Bosclair and Leggett (1989) found a relationship between growth of yellow perch, quantity and quality of food consumed, and fish community structure. They suggested that whole fish community average density is more important to perch growth than abundance measures of any single species. It may be possible that interactions between quantity and quality of prey items for juvenile striped bass and the density of the majority of fish in the fish community may be responsible for the variations in juvenile striped bass growth observed in this study. However, no indices of community structure were available to test this hypothesis.

No significant relationship was found between growth in mm/day and g/day and CPUE. However, on average, fast growth was associated with low abundances, variable growth rates were associated with intermediate abundances, and slower growth occurred at high abundances (>15 fish/haul). Trent (1962) and Tiller (1950) found no relationship between abundance and growth of young-of-the-year striped bass. Dey (1981) found a strong negative correlation between juvenile growth and abundance, and suggested that there may be a possibility of density-dependent growth in Hudson River striped bass populations. In the present study, a relationship is only observed when the extremely small and large populations are included in the analysis. An analysis considering only intermediate population sizes would conclude that growth was not density-dependent. It appears that a density-dependent effect on juvenile striped bass growth is occurring only at the extreme ranges of population size.

A significant positive linear relationship was found between abundance and mortality estimates of young-of-the-year striped bass. At catch-per-unit-effort values less than 15 fish/haul, mortality was similar for all rivers and year-classes. However, at a CPUE of close to 30 fish/haul, mortality increased to close to 4% loss/day, which might suggest a slight density-dependence during years of extremely high production. However, the possibility of the Rappahannock River in 1987 being an aberrant observation must be considered before fully accepting the concept of density-dependent mortality regulating juvenile striped bass populations.

The relationship between mortality and growth in either length or weight appears to be much more ambiguous than the relationships between each of these population parameters and abundance. When all rivers are included in the analysis, no relationship was found between mortality and growth rates in length or weight. However, due to the large overlap in the 95% confidence intervals, further estimates are needed on future populations of juvenile striped bass to provide a greater understanding of the relationships between growth and mortality.

Several authors have suggested that year-class strength of striped bass is controlled by environmental factors acting on early developmental stages (Cooper and Polgar 1981; Koo 1970; and Ulanowicz and Polgar 1980). Results of this study support the hypothesis that at least some of the major processes governing striped bass populations are density-dependent factors. Food availability, as measured by condition factor and average stomach fullness, appears to play a major role in controlling both growth and mortality of young-of-the-year striped bass. In the present study, it was also shown that density-dependent factors were important at extremely low, and even more notably, at extremely high abundances. Regulation of young-of-the-year striped bass populations appears to be partially controlled by density-dependent factors.

Chapter IV - Limitations of the back-calculation of length-at-age from daily growth increments, and application to juvenile striped bass populations.

INTRODUCTION

Since Pannella (1971) first described daily growth increments on fish otoliths, several authors have suggested that the growth history of individual fish can be reconstructed from the widths of otolith increments (Neilson and Geen 1982, 1985; Penney and Evans 1985; Wilson and Larkin 1982; and Volk et al 1984). For this technique to be valid, it must be shown that a relationship exists between growth of the otolith and somatic growth of the fish during the entire period of life history under study.

Some evidence exists that a consistent relationship between somatic and otolith growth may not always exist. Studies have shown that the otolith may continue to grow during periods of starvation or negative growth (Brothers 1981; Marshall and Parker 1982; Campana 1983; and Volk et al. 1984). Recently, Secor and Dean (1989), Secor et al. (1989), Reznick et al. (1989), and Mosegaard et al. (1988) provided direct evidence of an uncoupling between otolith and fish growth. Secor and Dean (1989), Secor et al. (1989), and Reznick et al. (1989) found that slower growing fish had larger otoliths at size and age than faster growing fish and concluded that somatic growth rate differences among individual fish may be responsible. These authors argue that the relationship may be population- or cohort-specific, as well as species-specific. Mosegaard et al. (1988) suggested that some metabolic activity may be responsible for growth of the otolith and that temperature effects on this metabolic activity may be the cause of the uncoupling between otolith and fish growth.

The present study was designed to evaluate the otolith-fish length relationships of several populations of juvenile striped bass and to determine the limitations of the back-calculation technique before application to wild populations.

MATERIALS AND METHODS

Juvenile striped bass were collected at the Harrison Lake Fish Hatchery from July to October in 1987 and from June to September in 1989. Field collections were made in 1986 and 1987 in conjunction with the Virginia Institute of Marine Science juvenile striped bass seine survey. Striped bass were collected in the James, Rappahannock, Mattaponi and Pamunkey Rivers in the manner described in Chapter III.

Otoliths were removed and processed in the transverse section as described in Chapter I. Measurements of otolith radius and individual increment widths were made with the BIOSONICS Optical Pattern Recognition System. Growth increments were distorted directly along the long axis of the otolith, therefore, increment widths were measured in very short transects along the edge of this distorted area (Figure 1.1). It was determined that the use of short segments did not have a large effect on measurements, since no trends were apparent when comparing measurements between segments. Otoliths for inclusion in the back-calculation of length-at-age were chosen subjectively based on the relative straightness of the transect used to measure growth increments.

The length L^i at an intermediate age i was back-calculated from otolith measurements from the formula:

$$L^i = (R^i - R^o) / (R^t - R^o) (SL - L^o) + L^o$$

where R^i is the width of the ith growth increment, R^o is the distance from the primordium to the first increment, R^t is the total radius along the long axis of the otolith, SL is standard length, and L^o is the size at hatch, estimated from the Y-intercept of the otolith radius-fish length relationship.

A Gompertz growth equation (Zweifel and Lasker 1976) was fit to the length-at-age data using nonlinear regression techniques. Growth equations were fit to pooled data and to data based on weekly hatching dates to determine if growth varied with hatching times.

RESULTS

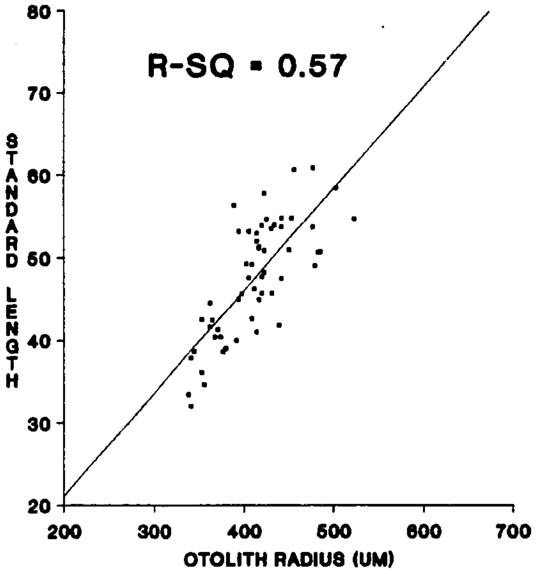
OTOLITH-FISH SIZE RELATIONSHIPS

Otolith radius-fish length relationships were calculated for the two years of hatchery data and each separate river population within each year (Figures 4.1 and 4.2). Sample sizes ranged from low values of 11 and 14 otoliths in the Pamunkey and Mattaponi River in 1986 to a high of 76 otoliths in the Pamunkey River in 1987 (Table 4.1). The relationships between otolith radius and fish length were modelled using least-squares linear regression procedures for all populations studied. There was a great deal of variability in the fit of the least-squares linear regression equations, however, all relationships were significant ($P<0.0001$). Coefficients of determination ranged from 0.11 in the Pamunkey River in 1986 to 0.84 in the Hatchery data in 1989 (Table 4.1), and all relationships were significant ($P<0.0001$). This variability does not appear to be an artifact of variations in sample size between populations. The Pamunkey River in 1986 had the lowest sample size at 11 otoliths and the lowest coefficient of determination at 0.11. The Pamunkey River in 1987, however, had the largest sample size at 76 otoliths and an intermediate coefficient of determination at 0.34. The best

Figure 4.1. Regression plots of standard length versus otolith radius for each river population in 1986.

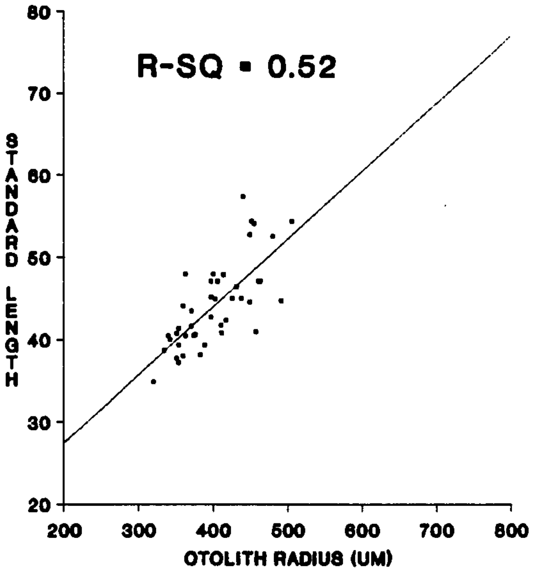
A

JAMES RIVER 1986



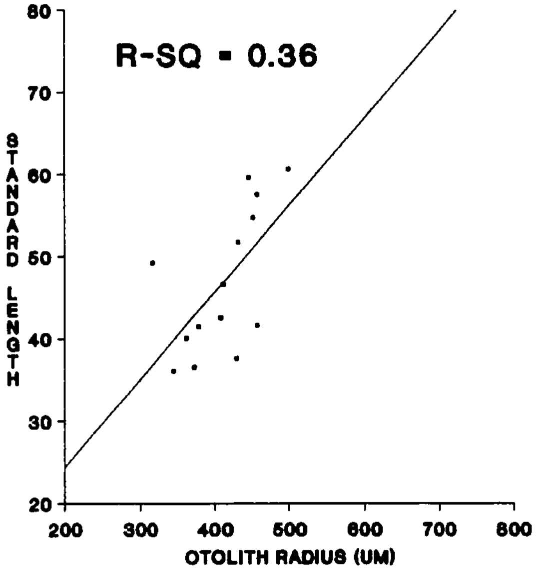
B

RAPPAHANNOCK RIVER 1986



C

MATTAPONI RIVER 1986



D

PAMUNKEY RIVER 1986

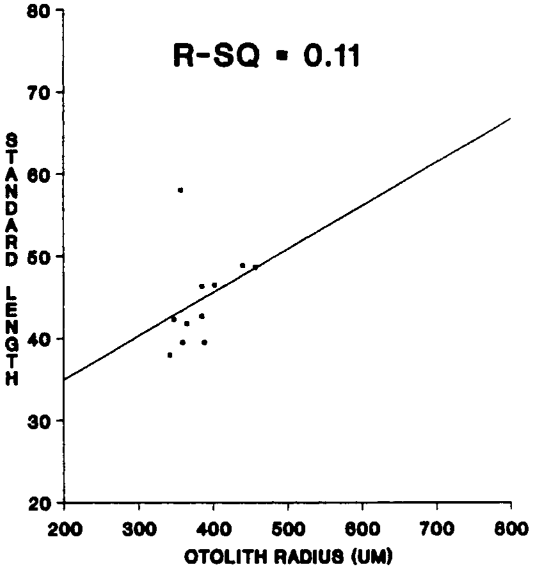
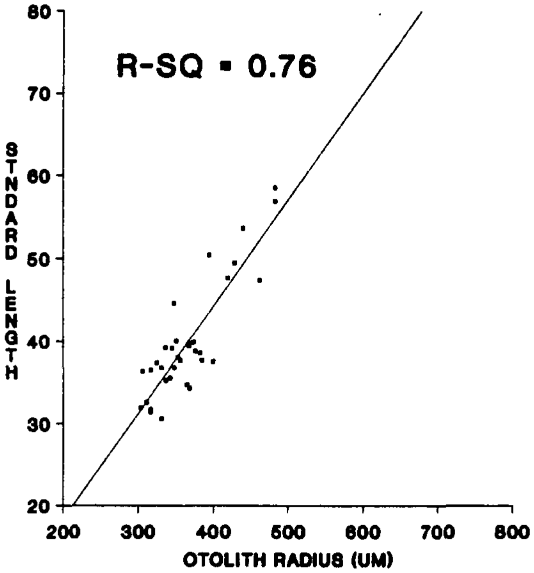


Figure 4.2. Regression plots of standard length versus otolith radius for each river population in 1987.

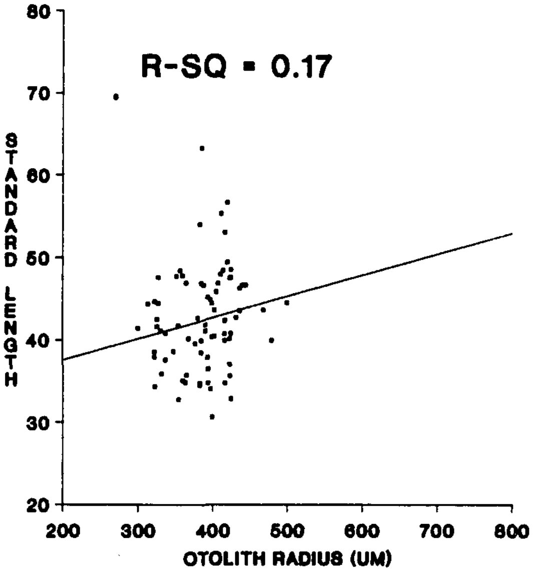
A

JAMES RIVER 1987



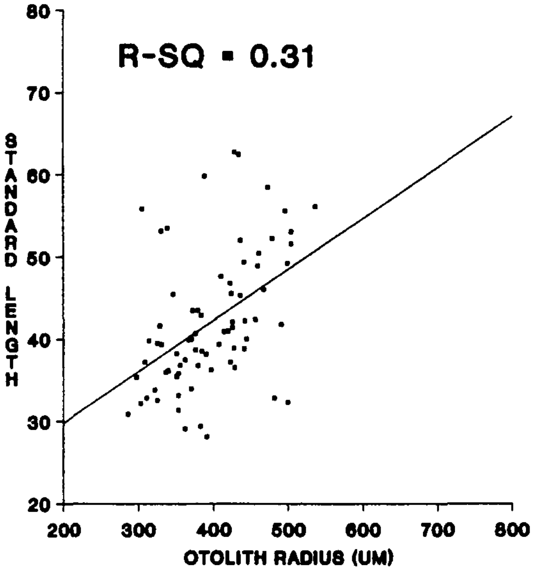
B

RAPPAHANNOCK RIVER 1987



C

MATTAPONI RIVER 1987



D

PAMUNKEY RIVER 1987

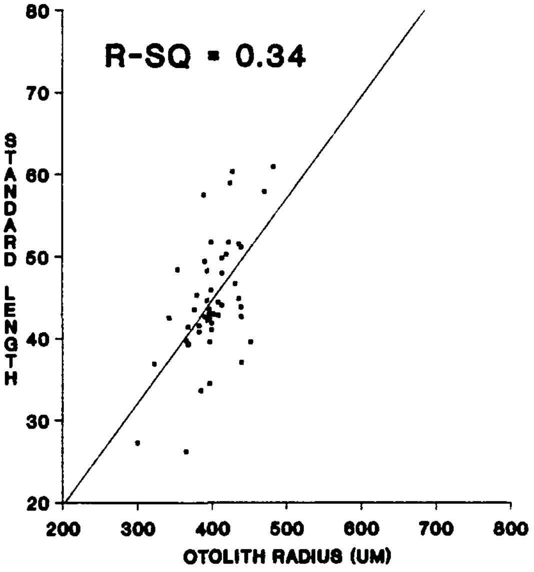


Table 4.1. Otolith-fish size relationships for the field-collected juvenile striped bass in each river population in 1986 and 1987, and for the 1987 and 1989 Harrison Lake Fish Hatchery data.

YEAR	RIVER	R-SQ	N	REGRESSION EQUATION
1986	JAMES	0.57	56	SL = 1.98 + 0.045(RADIUS)
	RAPP	0.52	44	SL = 1.23 + 0.063(RADIUS)
1987	JAMES	0.76	34	SL = 1.16 + 0.062(RADIUS)
	RAPP	0.17	74	SL = 1.96 + 0.042(RADIUS)
	MATT	0.31	49	SL = 1.72 + 0.050(RADIUS)
	PAM	0.34	76	SL = 1.00 + 0.022(RADIUS)
1987	HATCHERY	0.57	28	SL = 9.43 + 0.051(RADIUS)
1989	HATCHERY	0.84	22	SL = 7.21 + 0.058(RADIUS)

fit was provided by the 1989 Hatchery data, with a coefficient of determination of 0.84 and an intermediate sample size of 22 otoliths. Of the river populations, only the James River in 1987 had a coefficient of determination considered high enough to perform the back-calculation technique.

Analysis of covariance was used to compare the regressions from all populations. The analysis showed homogeneity of slopes (P=0.064), and no significant difference between regression equations for all populations studied (P=0.102).

Because daily growth increments are deposited on fish otoliths, even during periods of extremely slow somatic growth, the otolith of a slow growing fish may eventually reach a larger size than the otolith of a fast growing fish, even though the fish are the same size. The theory that growth rate differences among individual fish may have caused slower growing fish to have larger otoliths than faster growing fish of similar size was examined. Pairs of fish of similar length but of different known age were found in the 1987 and 1989 Hatchery data. To adjust for the slight differences in lengths of fish, the ratios of otolith radius to standard length were compared for each pair of fish. These data show that in 4 of the 5 pairs of fish, the older fish had a proportionately larger otolith than the younger fish (Table 4.2). In 1987 the two 175-day old fish had an otolith radius 2.4 and 8.0% larger than the two 156-day old fish. The same

Table 4.2 Pairs of hatchery-reared striped bass (Chapter I) showing standard length, otolith radius, the ratio of radius/standard length, and the per cent difference between ratios for each pair.

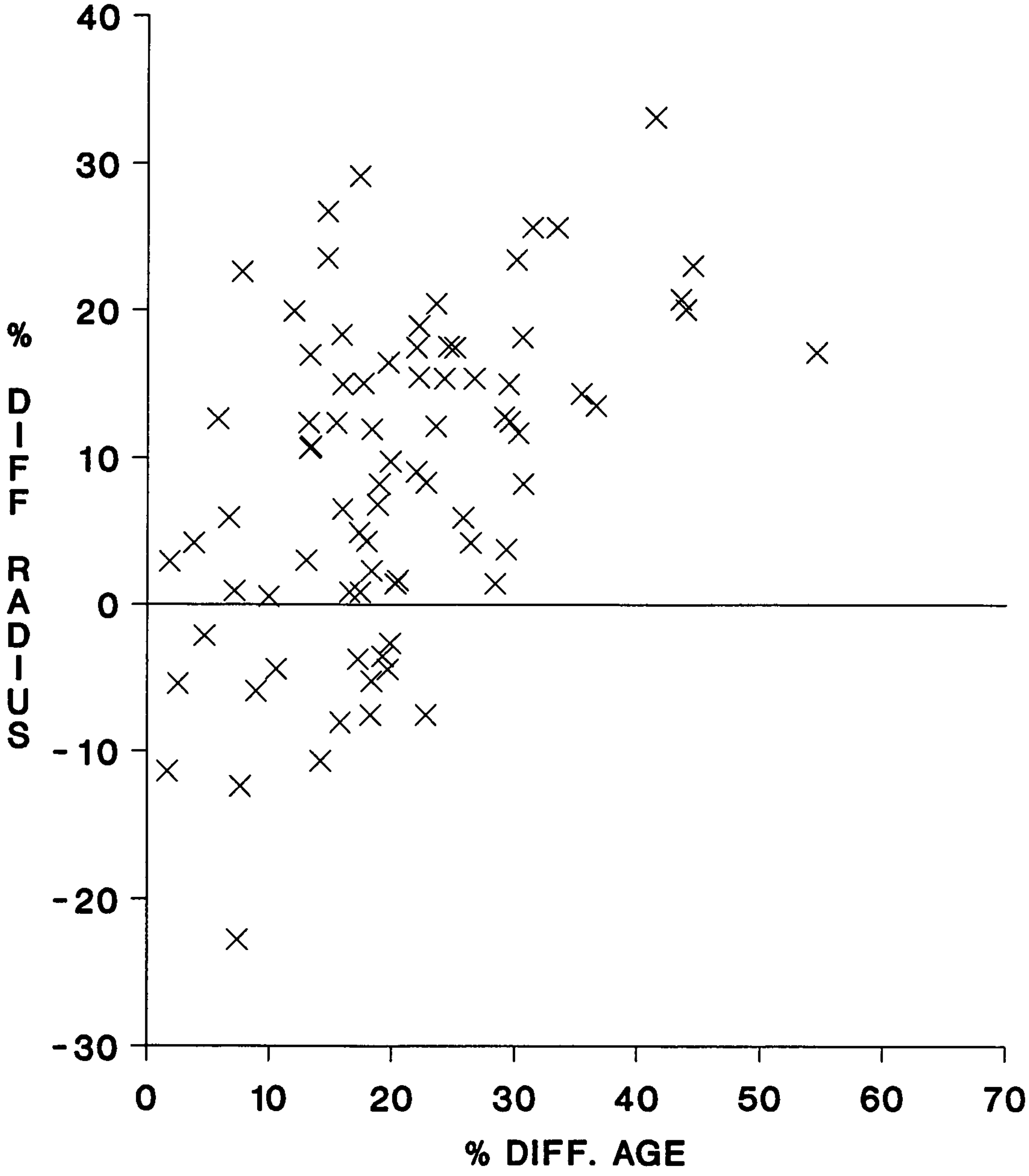
YEAR	AGE (days)	SL (mm)	RADIUS (um)	RATIO (RAD/SL)	%DIFF
1987	175	121.8	198	1.63	8.0
	156	120.4	180	1.50	
	175	101.1	168	1.66	2.4
	156	95.0	154	1.62	
1989	128	117.8	169	1.43	9.1
	114	118.1	154	1.30	
	86	71.0	126	1.77	14.7
	71	69.0	104	1.51	
	99	94.1	140	1.49	-2.0
	86	90.8	138	1.52	

pattern can be seen in 1989, with two of the older fish having an otolith radius 9.1 and 14.7% larger than the younger fish. Only in one pair of fish in 1989 did the older fish have an otolith radius smaller (2%) than the younger fish, showing that variability does exist between fish and otolith growth.

Seventy-six pairs of fish of similar size but different ages were found in the combined 1986-1987 field collected data. The per cent difference between otolith radius and the per cent difference between ages of fish were calculated for each pair and plotted (Figure 4.3). A positive per cent difference in otolith radius indicates that the older slower growing fish had a larger otolith than the younger faster growing fish. There is a positive trend to the data points, indicating that as the per cent difference between ages increases, the difference between otolith radii also increases. Sixty of the 76 data points, which is 78.9%, have a positive per cent difference between otolith radius, indicating that the majority of the slow growing fish have larger otoliths than the faster growing fish. At a per cent difference between ages greater than 30%, all of the older fish in each pair have larger otoliths.

If it is a correct assumption that a slow growing fish had a larger otolith than a fast growing fish of similar size, then it can be inferred that the slow growing fish should have positive residuals and the fast growing fish should have negative residuals in the otolith radius-fish length

Figure 4.3. Per cent difference in otolith radius versus per cent difference in ages for pairs of field-collected striped bass of similar size. All populations were pooled.


40
30
20
10
0
-10
-20
-30
% DIFF RADIUS
0
10
20
30
40
50
60
70
% DIFF. AGE

regressions (Figure 4.4). To test this hypothesis, the residuals of the otolith-fish size relationships were plotted against the predicted otolith radius (Figure 4.5). All populations were pooled since there was no significant difference between relationships. On average the slow growing fish (<0.4 mm/day) tended to have positive residuals (66.7%), while the fast growing fish (>0.7 mm/day) tended to have negative residuals (83.3%). However, there is a great deal of variability in the residuals, even among fish growing at average rates.

To further test the assumption that somatic growth rate differences affect the otolith-fish length relationships, fish in each river population were grouped by 0.1 mm/day growth rate intervals, with individual growth rates calculated as:

$$GR = (SL - 3.1) / \text{ESTIMATED AGE}$$

where GR is the average growth rate in mm/day for each individual fish over its lifespan, and SL is standard length of the fish. Otolith radius-fish length regressions were then calculated for separate growth rate groupings to determine if fish of similar somatic growth provide a better fit to the relationship. The Mattaponi and Pamunkey Rivers in 1986 were not included in this analysis due to small sample sizes.

Coefficients of determination for the majority of the relationships with a sample size greater than 5 had a better

Figure 4.4. Diagram of a typical linear otolith-fish size relationship illustrating the expected negative residuals for a fast growing fish and positive residuals for a slow growing fish.

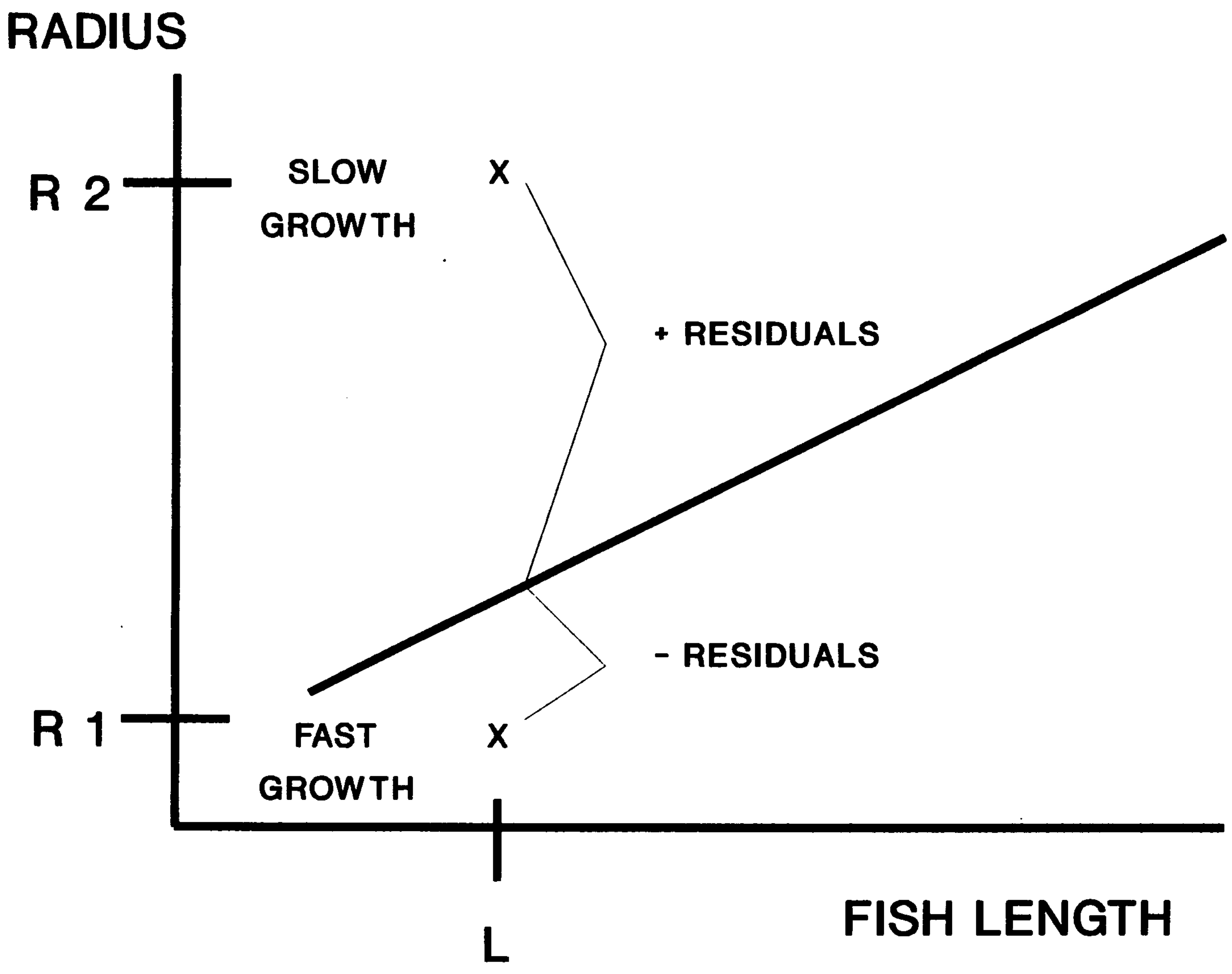
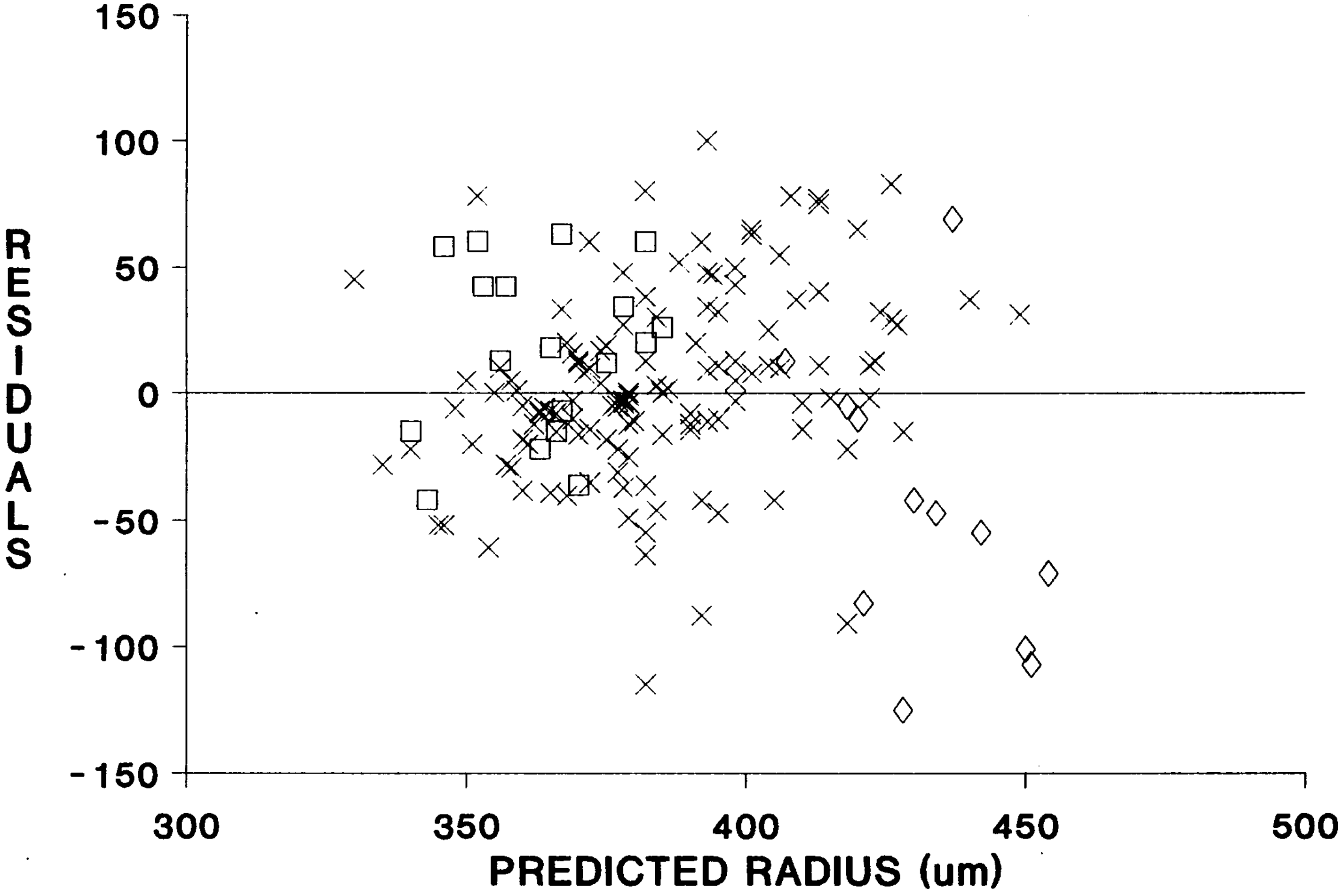

RADIUS
R 2
R 1
SLOW
GROWTH
FAST
GROWTH
X
X
+ RESIDUALS
- RESIDUALS
L
FISH LENGTH

Figure 4.5. Residuals from the otolith radius-fish length relationships versus predicted otolith radius for striped bass from all populations pooled, when fish were separated by individual growth rates in mm/day. (□ = <0.4 mm/day, X = 0.4-0.7 mm/day, ◇ = >0.7 mm/day)


RESIDUALS
150
100
50
0
-50
-100
-150
300
350
400
450
500
PREDICTED RADIUS (um)

fit than the overall relationship when all fish of variable growth rates were combined (Table 4.3). Total sample sizes are less than those listed in Table 4.1, since some fish with growth rates outside of the ranges reported in this analysis were excluded due to sample sizes being less than 5 in these groups. For example, the James River in 1986 had an overall coefficient of determination of 0.57. When the relationship was calculated for fish of similar somatic growth rates, the coefficients of determination increased to greater than 0.70 in all growth rate groupings. The Rappahannock River in 1987 had the second lowest overall coefficient of determination at 0.17. Grouping fish of similar somatic growth rates increased the coefficients of determination to greater than 0.5 in all cases. The coefficient of determination for the growth rate interval 0.5-0.6 mm/day in the James River in 1987 was less than the overall coefficient of determination when all fish of variable growth rates were combined. This may have been due to the large decrease in sample sizes for this group.

BACK-CALCULATION OF LENGTH-AT-AGE

Due to the poor fit of the otolith radius-fish length relationships for the majority of river populations, the back-calculation of length-at-age was only performed for the James River in 1987, which had a coefficient of determination of 0.76. A total of 16 otoliths were included in the analysis for the James River in 1987 (Table 4.4). Back-calculations

Table 4.3. Coefficients of determination for the otolith radius-fish length relationships for 0.1 mm/day growth rate intervals.

YEAR	RIVER	GROWTH INTERVAL	N	R-SQUARE
1986	JAMES	0.4-0.5	14	0.71
		0.5-0.6	14	0.73
		0.6-0.7	7	0.85
	RAPP	0.3-0.4	5	0.79
		0.4-0.5	30	0.59
1987	JAMES	0.5-0.6	6	0.66
	RAPP	0.4-0.5	18	0.56
		0.5-0.6	27	0.55
		0.6-0.7	8	0.57
	MATT	0.3-0.4	6	0.46
		0.4-0.5	22	0.68
		0.5-0.6	19	0.77
	PAM	0.4-0.5	8	0.53

Table 4.4. Summary data for 16 juvenile striped bass collected in the James River in 1987 and used in the back-calculation of length-at-age and growth rate-at-age.

SPECIMEN	COLLECTION DATE	AGE	BIRTHDATE	SL
1549	07 JULY	65	02 MAY	61.82
1551	07 JULY	52	15 MAY	45.13
1552	07 JULY	60	07 MAY	33.98
1554	07 JULY	54	13 MAY	34.47
1556	07 JULY	58	09 MAY	52.90
1576	07 JULY	64	03 MAY	36.26
1583	07 JULY	53	14 MAY	31.64
950	18 JUNE	39	10 MAY	23.50
952	18 JUNE	38	11 MAY	29.17
953	18 JUNE	34	15 MAY	20.53
973	18 JUNE	34	15 MAY	22.00
985	18 JUNE	38	11 MAY	19.60
1651	03 AUG	86	09 MAY	45.20
1653	03 AUG	79	16 MAY	40.23
1654	03 AUG	92	03 MAY	56.42
1712	24 AUG	94	22 MAY	69.97

of length-at-age and growth rate-at-age were only performed on otoliths which provided a relatively straight transect from the primordium to the edge of the otolith, thereby limiting the sample size to only 16 otoliths. Lengths of fish included in this analysis ranged from 19.60 mm to 69.97 mm standard length and ages ranged from 34 days to 94 days (Table 4.4).

The Gompertz growth equation for all 16 fish is shown in Table 4.5. Length at hatch was estimated from this equation at 2.87 mm. Length-at-age and growth rate-at-age in mm/day and %/day for weekly intervals are presented in Table 4.6 and Figures 4.6 A. Growth rates in mm/day increased from 0-28 days from 0.387 to 0.690 mm/day (Figure 4.6 B). After 28 days, growth rates decreased before reaching 0.161 mm/day at 98 days of age. The average growth rate for the 98 days of growth was estimated at 0.421 mm/day. Growth in %/day decreased throughout the period from 6.9-0.3 %/day. Lower 95% confidence intervals about the back-calculated lengths were relatively small for all ages, however, upper 95% confidence intervals tended to increase with increasing age (Table 4.6).

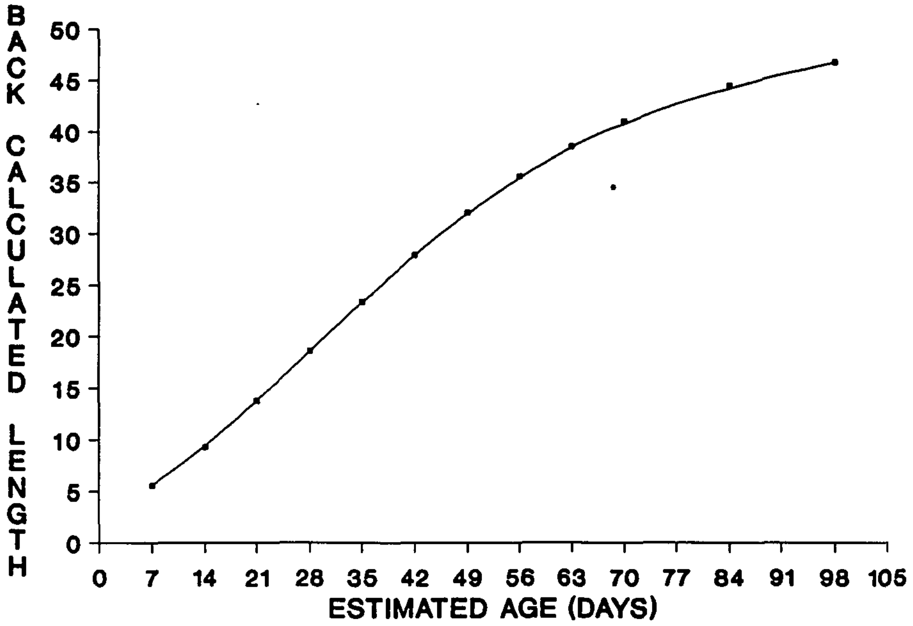
Each fish was placed in a weekly birthdate group by subtracting the age of the fish from the collection date. Birthdates ranged from May 1-May 21 for the fish included in this analysis (Table 4.4). Gompertz growth equations for the separate groupings are shown in Table 4.5. Length at hatch, again estimated from the Gompertz growth equations ranged from 2.53-2.83 mm. Lengths at hatch calculated for fish in the

Table 4.5. Gompertz growth equations for 16 juvenile striped bass collected in the James River in 1987, and for data based on weekly birthdate intervals.

DATE	N	GOMPERTZ EQUATION
ALL DATE	16	$L_t = 2.87\ e^{2.962\ (1 - e^{-(0.039)t}}$
MAY 1-7	4	$L_t = 2.70\ e^{3.069\ (1 - e^{-(0.042)t}}$
MAY 8-14	7	$L_t = 2.53\ e^{2.964\ (1 - e^{-(0.045)t}}$
MAY 15-21	5	$L_t = 2.83\ e^{3.146\ (1 - e^{-(0.039)t}}$

Figure 4.6. A: Back-calculated length-at-age from the Gompertz growth equation for 16 fish in the James River in 1987 when all birthdates were combined, and B: Growth rate-at-age in mm/day from the Gompertz growth equation for 16 fish from the James River in 1987, when all birthdates were combined.

A


BACK CALCULATED LENGTH
50
45
40
35
30
25
20
15
10
5
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

B

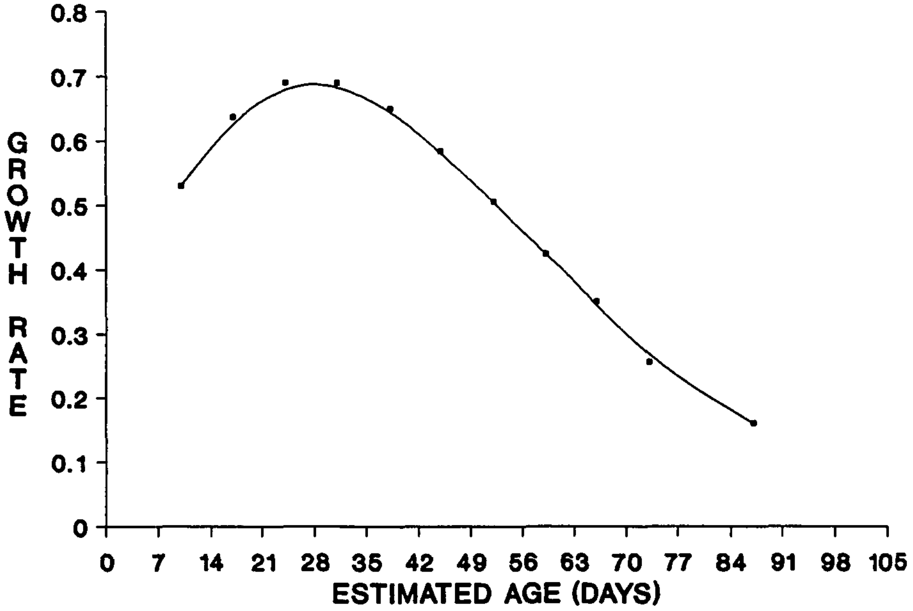

GROWTH RATE
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

Table 4.6. Back-calculated length-at-age and growth rates-at-age in mm/day and %/day for 16 juvenile striped bass collected in the James River in 1987.

AGE	LOWER 95%	MEAN	UPPER 95%	MM/DAY	%/DAY
1		2.87			
7	5.22	5.58	6.07	0.387	6.9
14	8.55	9.29	10.35	0.530	5.7
21	12.55	13.75	15.50	0.637	4.6
28	16.87	18.58	21.06	0.680	3.7
35	21.20	23.41	26.57	0.690	2.9
42	25.31	27.92	31.67	0.650	2.3
49	29.02	32.05	36.19	0.584	1.8
56	32.25	35.59	40.03	0.506	1.4
63	35.00	38.56	43.22	0.424	1.1
70	37.29	41.02	45.80	0.351	0.9
84	40.66	44.61	49.47	0.256	0.6
98	42.83	46.87	51.71	0.161	0.3

separate birthdate groupings were all lower than was estimated when all fish were combined, however, values were very similar. Length-at-age and growth rates-at-age are presented in Table 4.7-4.9, and Figures 4.7 and 4.8. The pattern of growth is similar for all birthdate groupings, however, maximum growth rates were reached at different ages. Maximum growth rates of 0.779 mm/day an 0.706 mm/day were reached by age 28 for fish hatched between May 1-7 and May 8-14, and a maximum growth rate of 0.813 mm/day was reached at age 35 for fish hatched between May 15-21 (Figures 4.7 and 4.8). Lengths-at-age were smaller and growth rates-at-age were slower at all ages for fish hatched between May 8-14 (Figure 4.8). Lengths-at-age at all ages were greatest for fish hatched between May 15-21 (Figure 4.7), however, growth rates-at-age were slower for the first 14 days when compared to fish hatched between May 1-7 (Figure 4.8). Due to the similarities in lengths-at-age and growth rates-at-age for the birthdate groupings, and the pooling of the data over weekly periods, data on variations in growth rates over time are inconclusive.

Standard lengths-at-capture were calculated from all fish aged in the James River in 1987 and overlaid with the Gompertz growth equation calculated from the 16 fish analyzed (Figure 4.9). Lengths-at-capture for fish less than approximately 50 days old corresponded well with the Gompertz growth curve, however, variability in standard lengths increased after about 50 days of age. The Gompertz growth curve after 50 days

Table 4.7. Back-calculated length-at-age and growth rates-at-age in mm/day and %/day for juvenile striped bass collected in the James River in 1987 and hatched between 1-7 May.

AGE	L (t)	MM/DAY	%/DAY
1	2.70		
7	5.63	0.419	7.4
14	9.78	0.593	6.1
21	14.82	0.720	4.9
28	20.27	0.779	3.8
35	25.65	0.769	3.0
42	30.63	0.711	2.3
49	35.00	0.624	1.8
56	38.69	0.527	1.4
63	41.73	0.434	1.0
70	44.17	0.349	0.8
84	47.61	0.246	0.5
98	49.67	0.147	0.3

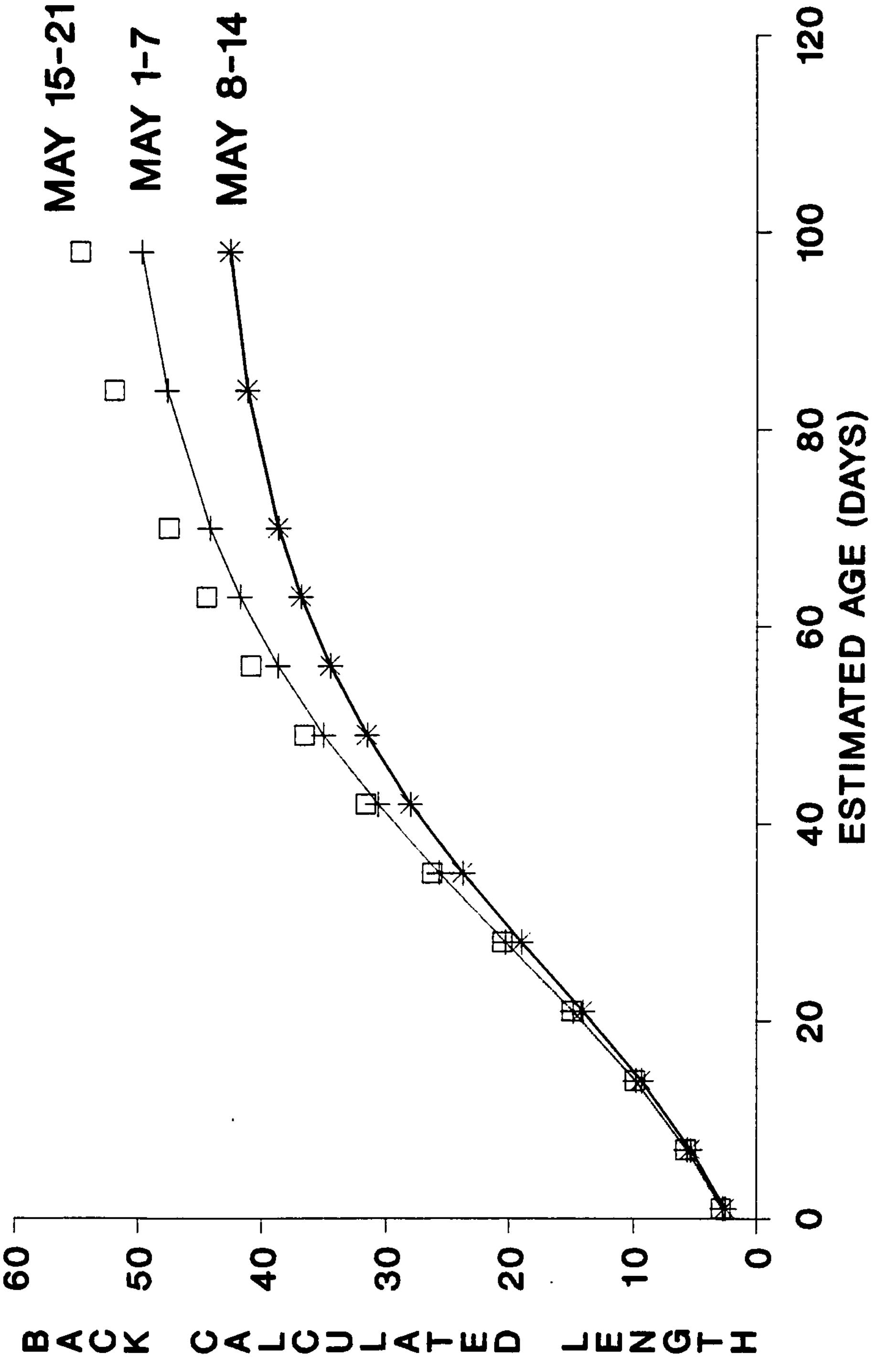
Table 4.8. Back-calculated length-at-age and growth rates-at-age in mm/day and %/day for juvenile striped bass collected in the James River in 1987 and hatched between 8-14 May.

AGE	L (t)	MM/DAY	%/DAY
1	2.53		
7	5.36	0.404	7.5
14	9.34	0.569	6.12
21	14.05	0.673	4.8
28	18.99	0.706	3.7
35	23.72	0.676	2.8
42	27.95	0.604	2.2
49	31.53	0.511	1.6
56	34.47	0.420	1.2
63	36.82	0.336	0.9
70	38.64	0.260	0.7
84	41.12	0.177	0.4
98	42.53	0.101	0.2

Table 4.9. Back-calculated length-at-age and growth rates-at-age in mm/day and %/day for juvenile striped bass collected in the James River in 1987 and hatched between 15-21 May.

AGE	L (t)	MM/DAY	%/DAY
1	2.83		
7	5.72	0.413	7.2
14	9.83	0.587	6.0
21	14.90	0.724	4.9
28	20.50	0.800	3.9
35	26.19	0.813	3.1
42	31.62	0.776	2.5
49	36.53	0.701	1.9
56	40.82	0.613	1.5
63	44.45	0.519	1.2
70	47.46	0.430	0.9
84	51.87	0.315	0.6
98	54.66	0.199	0.4

Figure 4.7. Length-at-age from the Gompertz growth equation for James River 1987 striped bass separated into weekly birthdate intervals from May 1-21.



BACK CALCULATED LENGTH
0
10
20
30
40
50
60
ESTIMATED AGE (DAYS)
0
20
40
60
80
100
120
□ MAY 15-21
+ MAY 1-7
✳ MAY 8-14

Figure 4.8. Growth rate-at-age in mm/day from the Gompertz growth equation for James River 1987 striped bass separated into weekly birthdate intervals from May 1-21.

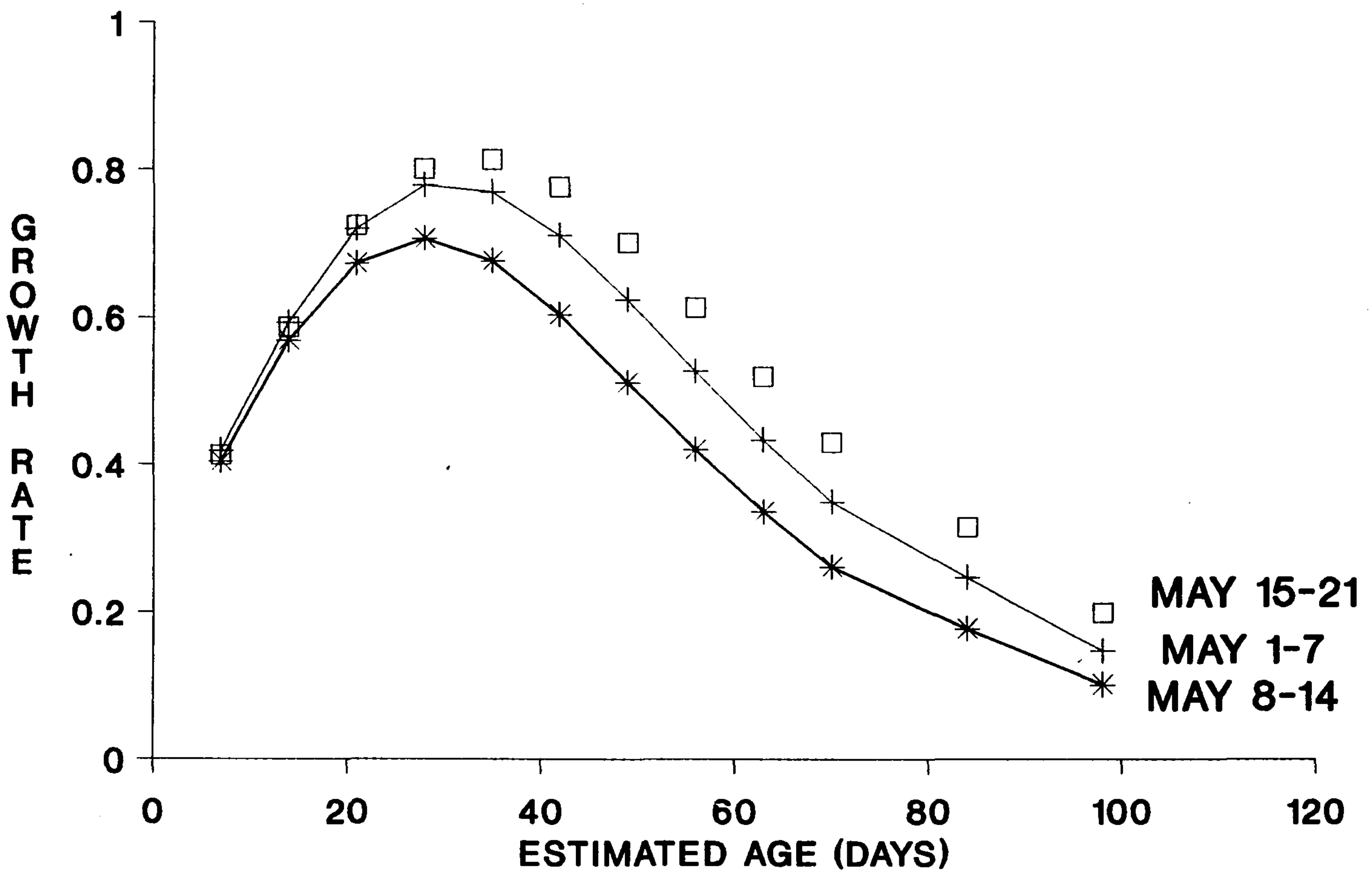
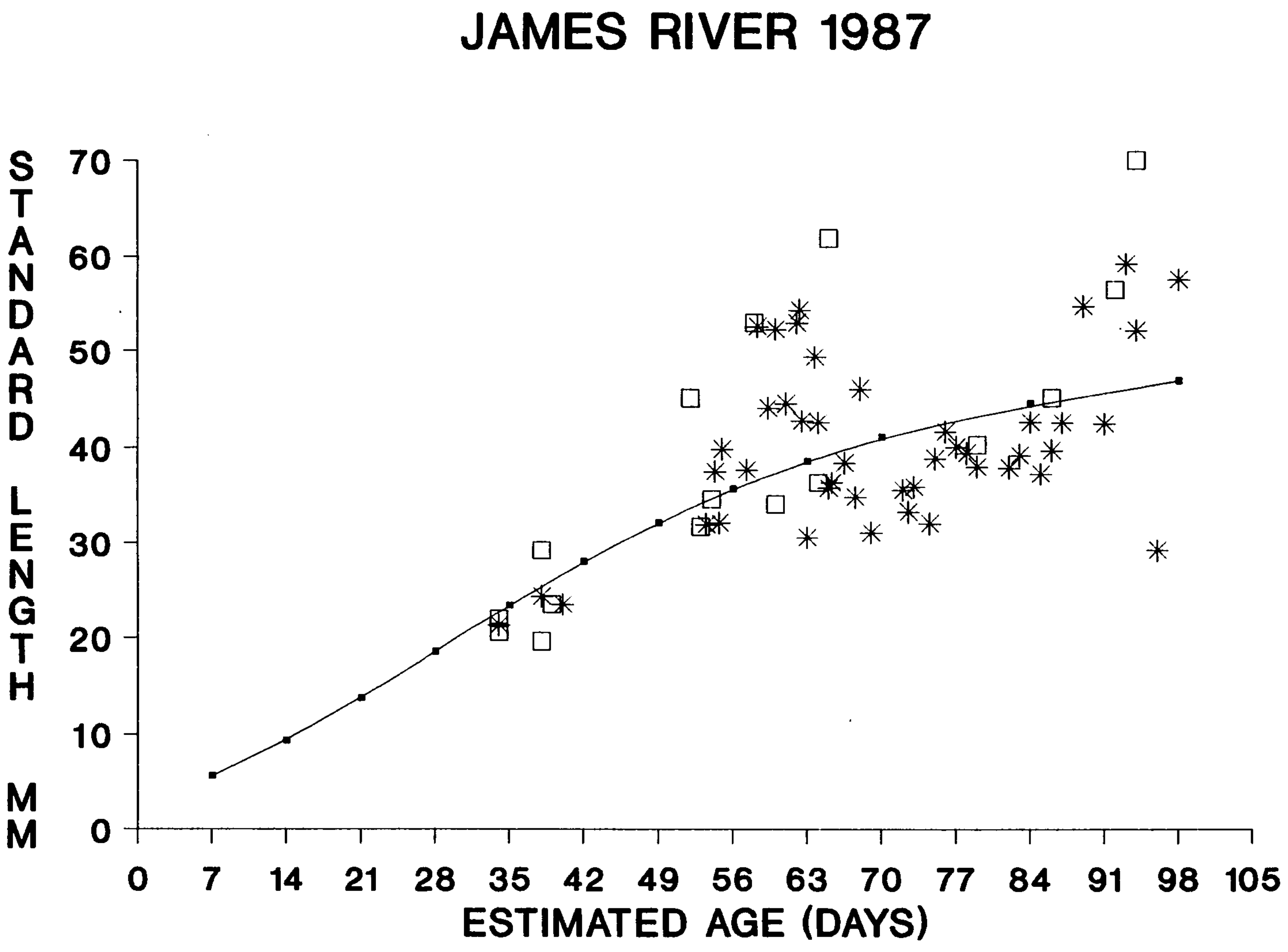

GROWTH RATE
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
ESTIMATED AGE (DAYS)
MAY 15-21
MAY 1-7
MAY 8-14

Figure 4.9. Comparison of the Gompertz growth equation from 16 James River 1987 striped bass and mean lengths-at capture for all fish collected in the James River in 1987. (□ = fish used to calculate Gompertz growth equation, X = mean lengths for all fish collected).


JAMES RIVER 1987
STANDARD LENGTH MM
70
60
50
40
30
20
10
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

appeared to correspond reasonably well with the average lengths at successive ages after this period. However, when considering the length-at-age data for the 16 fish used in this analysis, it appears that the back-calculated Gompertz growth curve estimates the lower range of lengths only. The upper 95% confidence intervals about the predicted length-at-age from the Gompertz growth equation also expand with increasing age (Table 4.6).

This same pattern holds for fish separated into birthdate groupings (Figures 4.10-4.12). The Gompertz growth curve appeared to follow the same pattern when compared to standard lengths-at-capture for all birthdate groupings. Lengths-at-capture for fish less than approximately 50 days of age corresponded well with the Gompertz growth curve for all groupings, however, variability in standard lengths-at-capture again increased with increasing age.

Figures 4.13-4.15 present the back-calculated lengths-at-age for each individual fish overlaid with the Gompertz growth curve calculated for fish in their respective birthdate grouping. It is apparent from each of these Figures that the Gompertz growth equation accurately describes the growth of striped bass only during the very early life history of this species (approximately 30 days). The Gompertz growth curve appears to approach an asymptotic length which does not correspond to the back-calculated lengths-at-age for individual fish. The Gompertz equation describes a period of

Figure 4.10. Comparison of the Gompertz growth equation from 4 James River 1987 striped bass hatched between May 1-7 and mean lengths-at-capture for all fish in the James River in 1987 hatched between May 1-7 (☐ = fish used to calculate the Gompertz growth equation, X = mean lengths for all fish collected hatched between May 1-7).

MAY 1-7

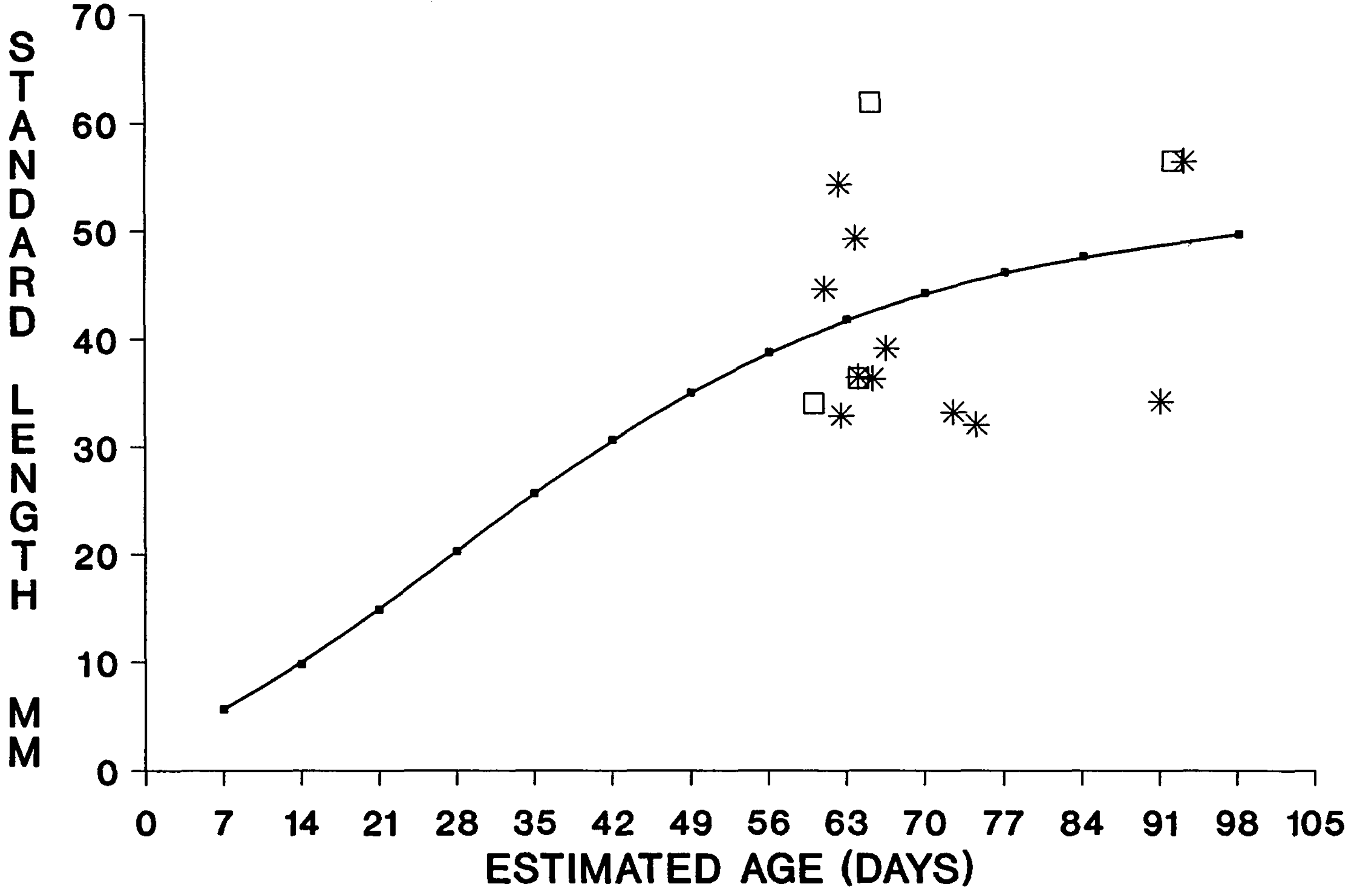
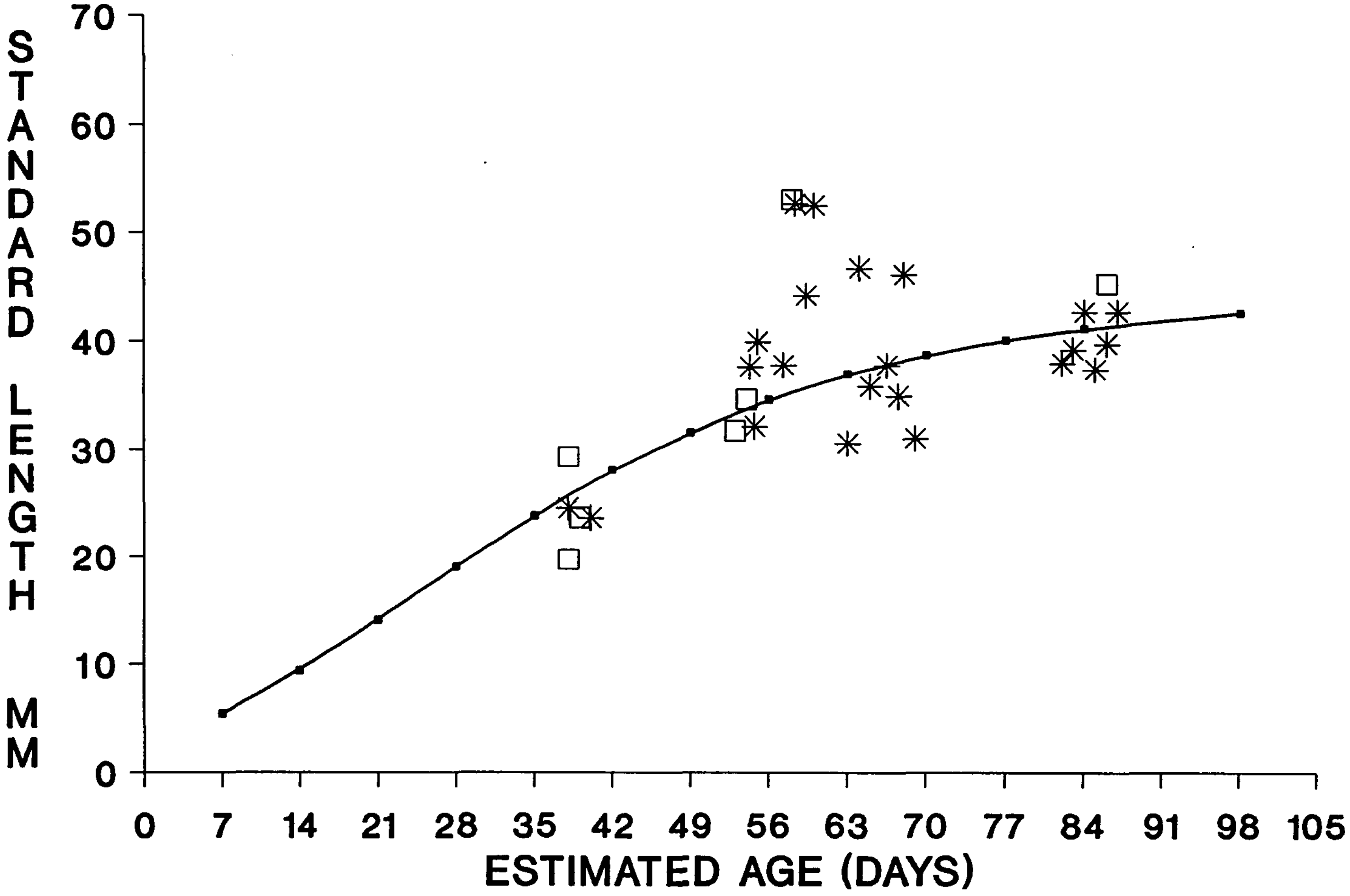

STANDARD LENGTH MM
70
60
50
40
30
20
10
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

Figure 4.11. Comparison of the Gompertz growth equation from 7 James River 1987 striped bass hatched between May 8-14 and mean lengths-at-capture for all fish in the James River in 1987 hatched between May 8-14 (□ = fish used to calculate the Gompertz growth equation, X = mean lengths of all fish collected hatched between May 8-14).



MAY 8-14

STANDARD LENGTH MM
70
60
50
40
30
20
10
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

Figure 4.12. Comparison of the Gompertz growth equation from 5 James River 1987 striped bass hatched between May 15-21 and mean lengths-at-capture for all fish in the James River in 1987 hatched between May 15-21 (□ = fish used to calculate the Gompertz growth equation, X = mean lengths of all fish collected hatched between May 15-21).

MAY 15-21

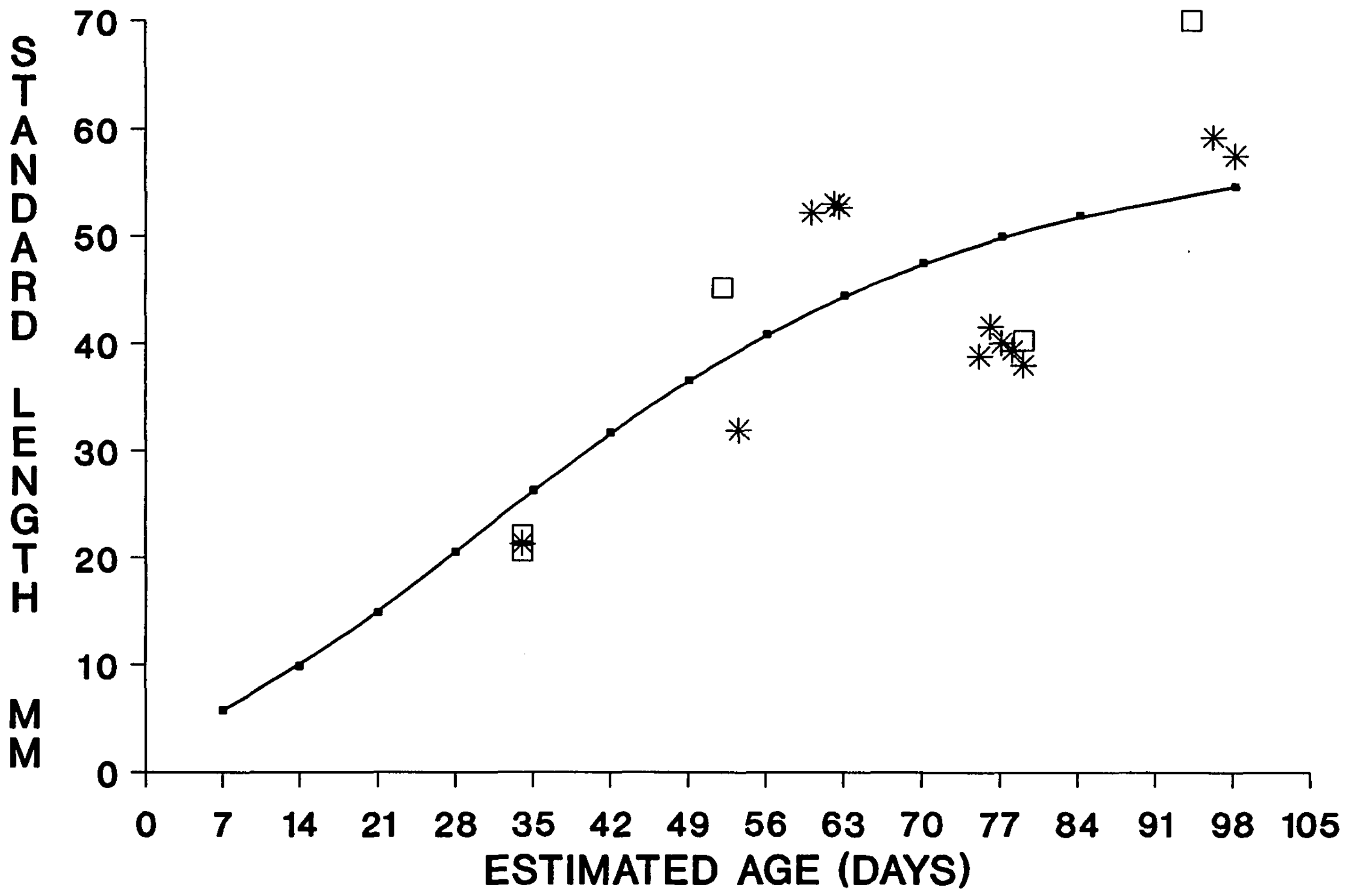

STANDARD LENGTH MM
70
60
50
40
30
20
10
0
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
ESTIMATED AGE (DAYS)

Figure 4.13. Back-calculated lengths for individual striped bass hatched between May 1-7, overlaid with the Gompertz growth curve calculated for the same fish.

MAY 1-7

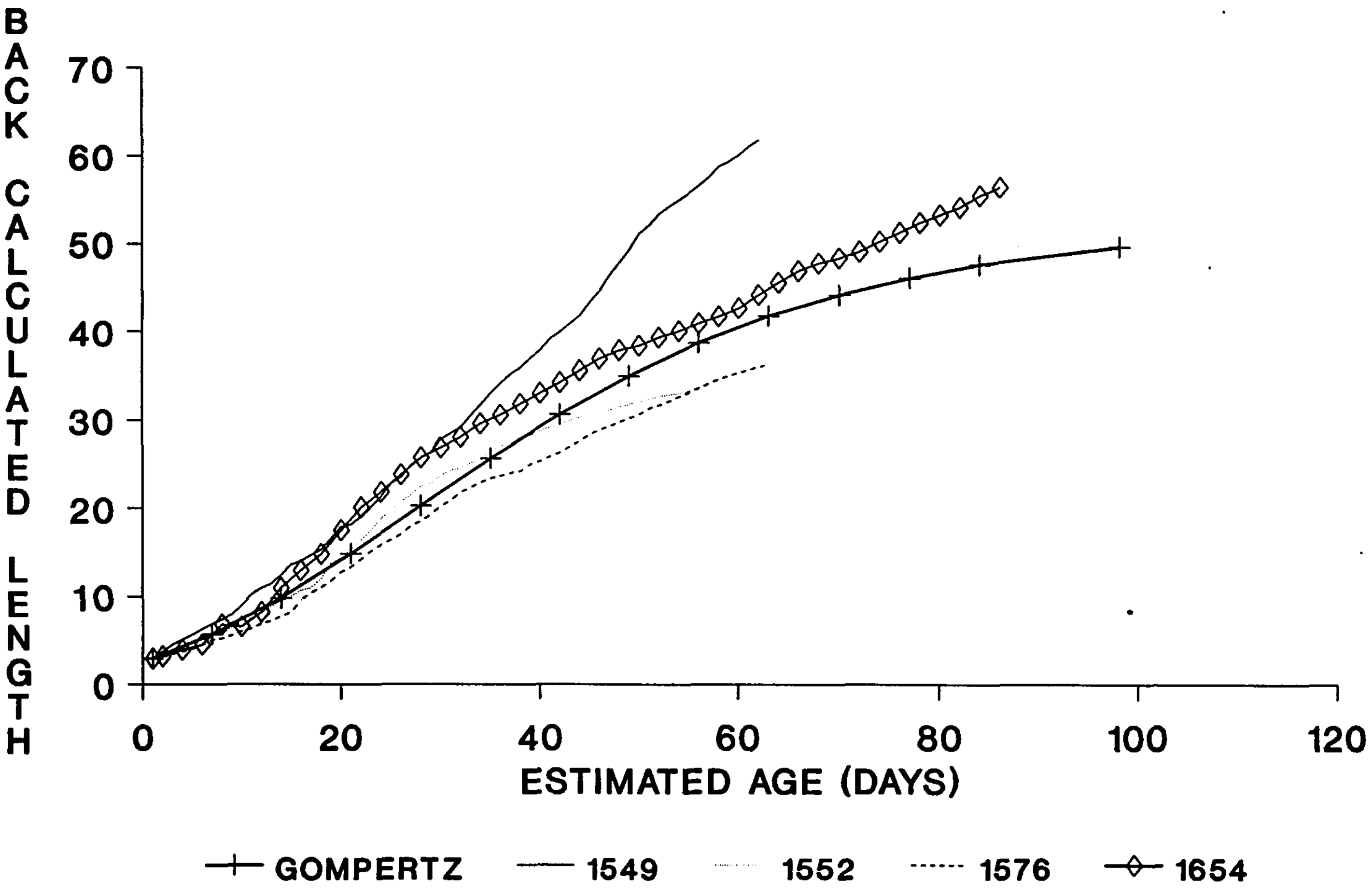
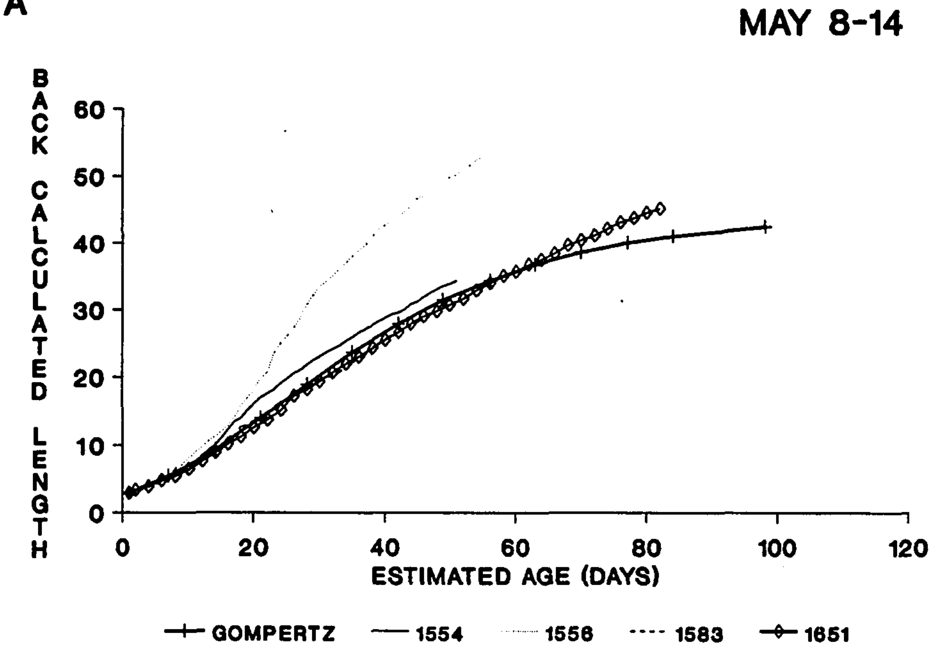

BACK CALCULATED LENGTH
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
ESTIMATED AGE (DAYS)
GOMPERTZ
1549
1552
1576
1654

Figure 4.14. Back-calculated lengths for individual striped bass hatched between May 8-14, overlaid with the Gompertz growth curve calculated for the same fish.

A


MAY 8-14
BACK CALCULATED LENGTH
60
50
40
30
20
10
0
0
20
40
60
80
100
120
ESTIMATED AGE (DAYS)
GOMPERTZ
1554
1556
1583
1651

B

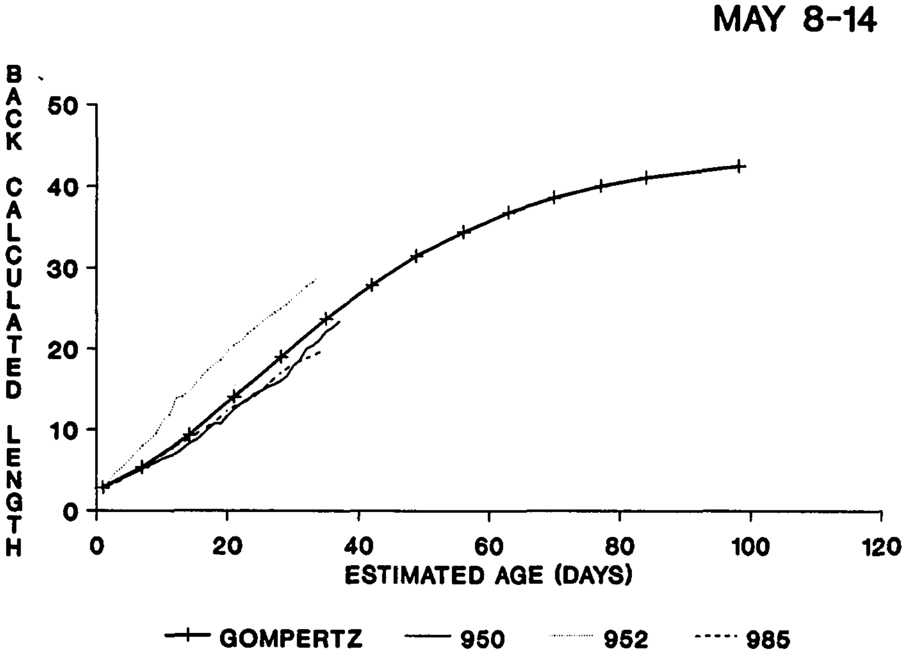
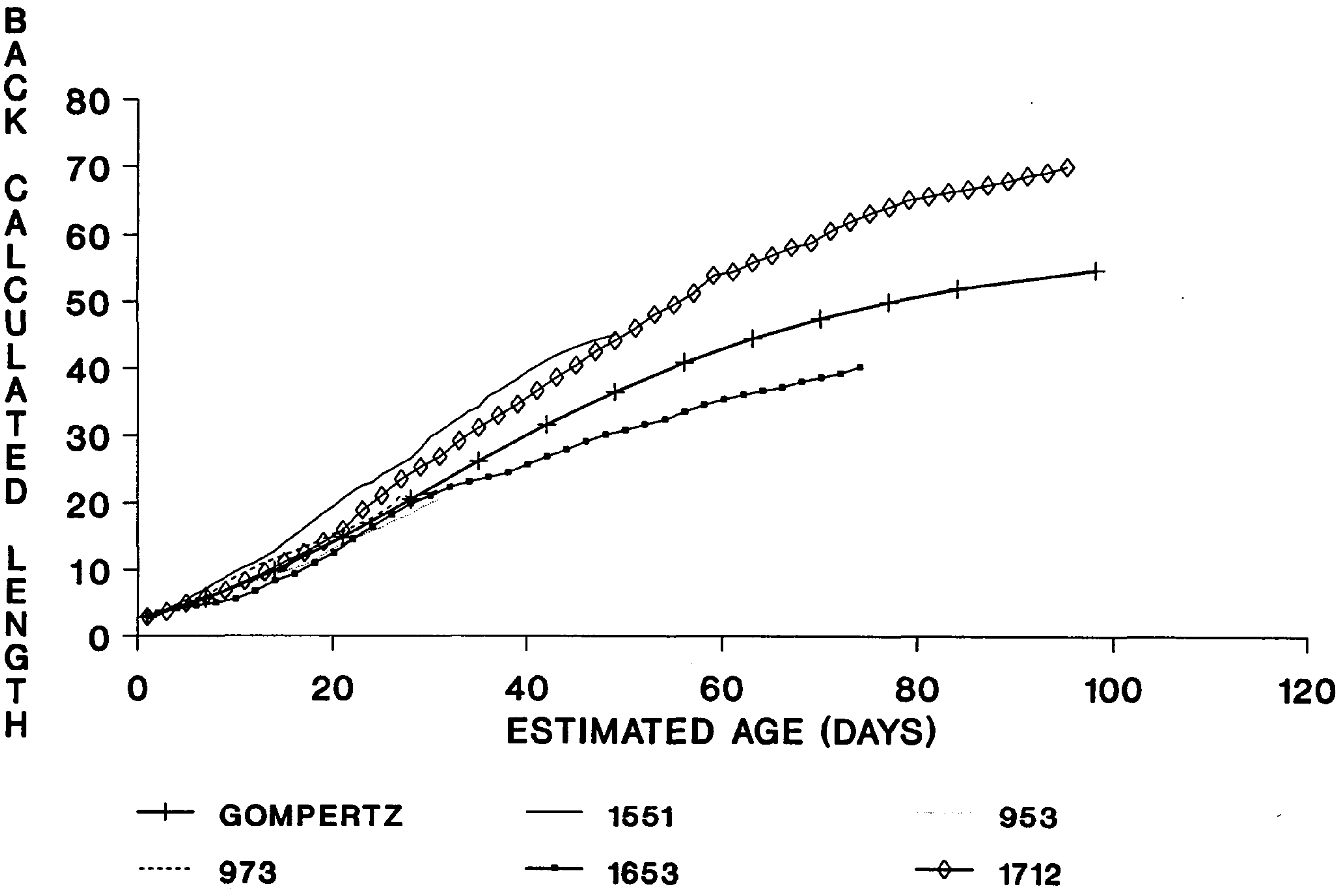

MAY 8-14
BACK CALCULATED LENGTH
50
40
30
20
10
0
0
20
40
60
80
100
120
ESTIMATED AGE (DAYS)
GOMPERTZ
950
952
985

Figure 4.15. Back-calculated lengths for individual striped bass hatched between May 15-21, overlaid with the Gompertz growth curve calculated for the same fish.

MAY 15-21


BACK CALCULATED LENGTH
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
ESTIMATED AGE (DAYS)
GOMPERTZ
1551
953
973
1653
1712

slowing growth rates after about 80 days, while it is apparent from the back-calculated lengths-at-age for the individual fish that growth rates do not decrease as rapidly as described by the Gompertz growth equation.

SIZE-SELECTIVE MORTALITY

The potential for size-selective mortality was evaluated by calculating mean back-calculated lengths at 7 day intervals up to 35 days for 8 fish between 20-40 mm standard length and 4 fish 50-70 mm standard length. Mean back-calculated lengths were consistently lower at all ages for fish between 20-40 mm (Table 4.10), indicating an apparent 'reverse' Lee's phenomenon. Back-calculated lengths calculated were similar at 7 days of age at 5.8 mm for 20-40 mm fish and 6.0 mm for fish 50-70 mm in length. However, by 35 days of age the back-calculated length from the 20-40 mm fish was lower at 23.9 mm, compared to a back-calculated length of 33.2 mm from fish 50-70 mm in length. However, the small sample sizes included in this analysis preclude any definitive conclusions on size-selective mortality in the James River in 1987.

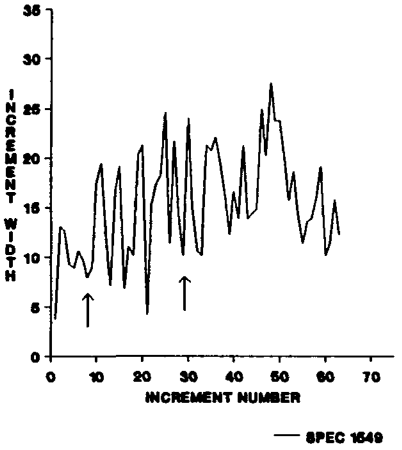
STRESS PERIODS

Increment widths were plotted by increment number for all 16 fish to determine if stress periods occurred in the life history of fish included in the analysis (Figures 4.16-4.19). Decreases in increment widths were apparent in all otoliths

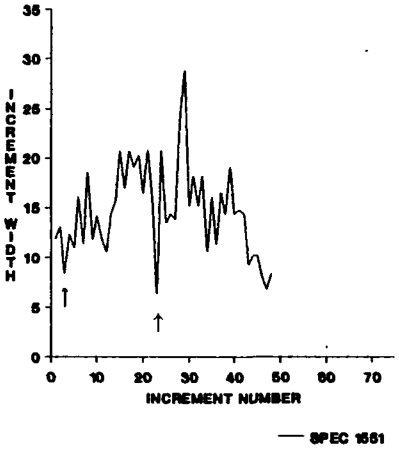
Table 4.10. Back-calculated length-at-age for juvenile striped bass between 20-40 mm SL and 50-70 mm SL.

AGE	LENGTH (20-40 MM FISH)	LENGTH (50-70 MM FISH)
7	5.8	6.0
14	9.8	11.3
21	14.7	18.4
28	19.4	26.5
35	23.9	33.2

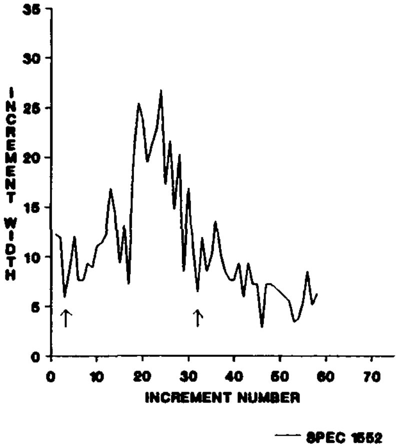
Figure 4.16. Mean increment widths by increment number for 4 fish from the James River in 1987. Arrows mark rapid decreases in increment widths, possible signifying first feeding at 3-10 days and metamorphosis at 28-35 days.



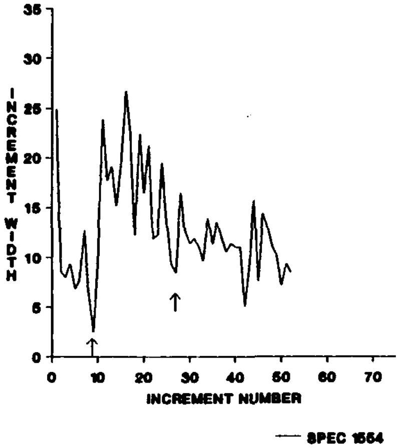
INCREMENT WIDTH
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1549



INCREMENT WIDTH
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1551

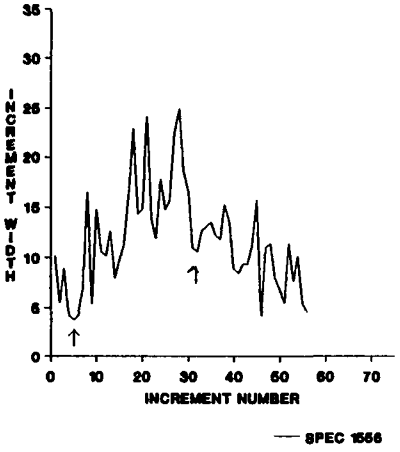


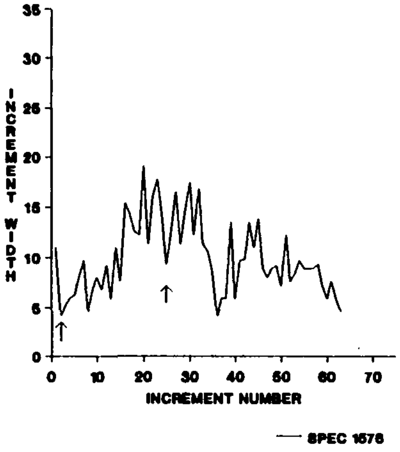
INCREMENT WIDTH
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1552

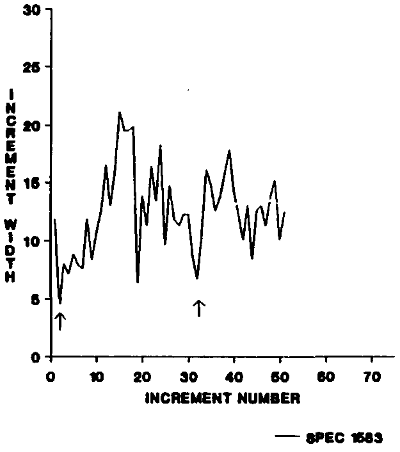


INCREMENT WIDTH
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1554

Figure 4.17. Mean increment widths by increment number for 4 fish from the James River in 1987. Arrows mark rapid decrease in increment widths, possibly signifying first feeding at 3-10 days and metamorphosis at 28-35 days.


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1566


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1576


INCREMENT WIDTH
0
5
10
15
20
25
30
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 1583

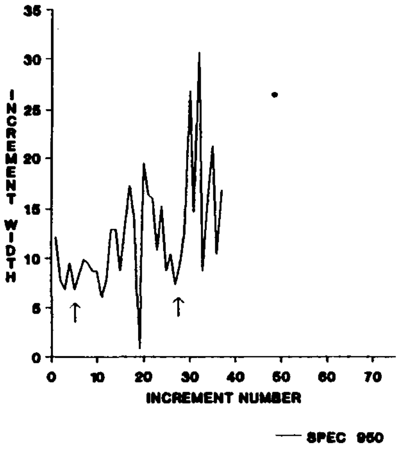
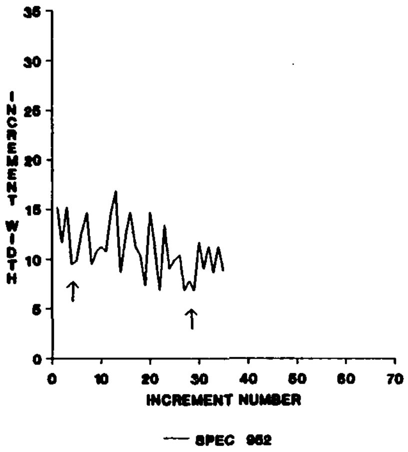
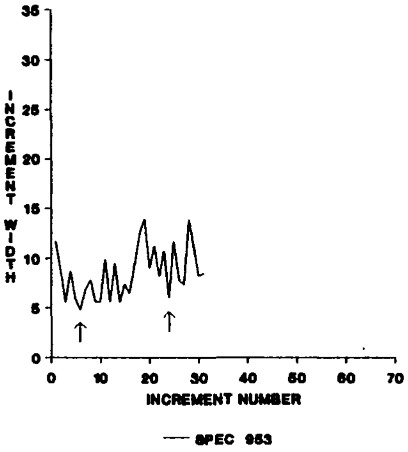
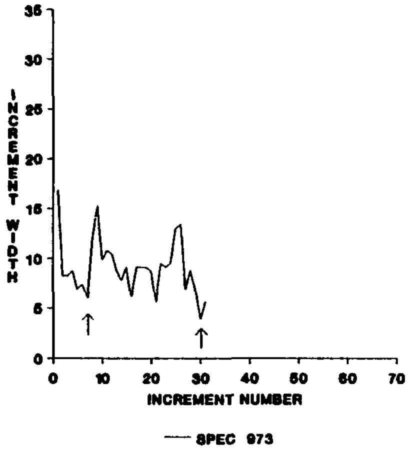

INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 950

Figure 4.19. Mean increment widths by increment number for 4 fish from the James River in 1987. Arrows mark rapid decrease in increment widths, possibly signifying first feeding at 3-10 days and metamorphosis at 28-35 days.


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 962


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 953


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 973

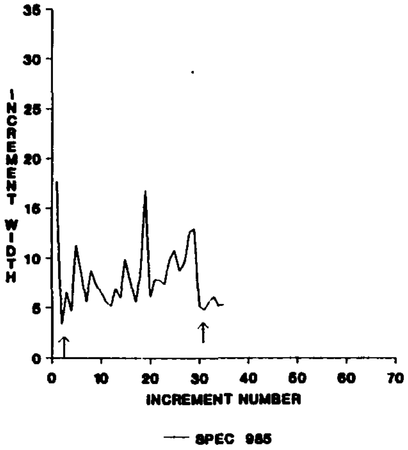
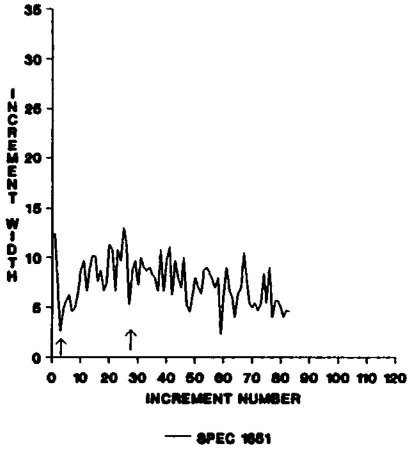
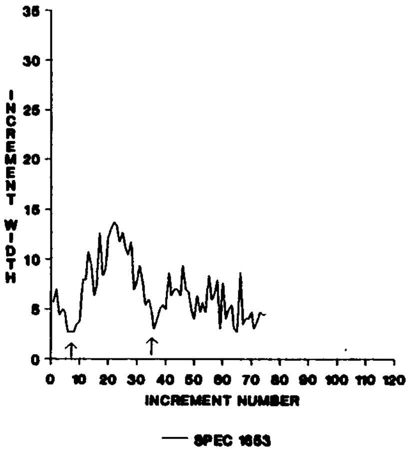
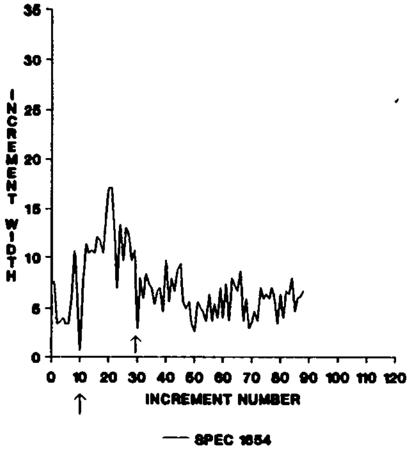
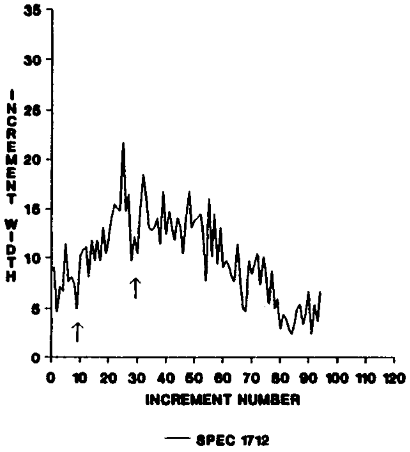

INCREMENT WIDTH
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
INCREMENT NUMBER
SPEC 985

Figure 4.19. Mean increment widths by increment number for 4 fish from the James River in 1987. Arrows mark rapid decrease in increment widths, possibly signifying first feeding at 3-10 days and metamorphosis at 28-35 days.


INCREMENT WIDTH
0
5
10
15
20
25
30
35
0 10 20 30 40 50 60 70 80 90 100 110 120
INCREMENT NUMBER
SPEC 1651

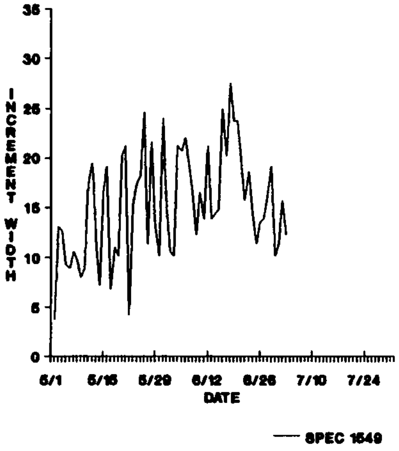

INCREMENT WIDTH
0
5
10
15
20
25
30
35
0 10 20 30 40 50 60 70 80 90 100 110 120
INCREMENT NUMBER
SPEC 1653

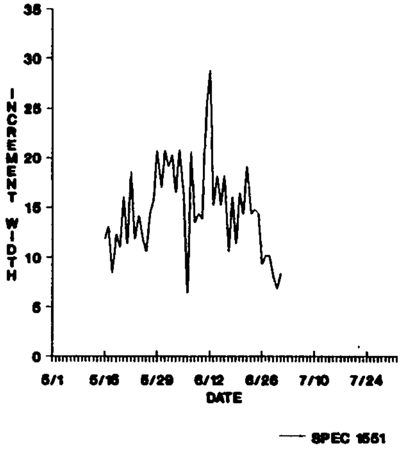

INCREMENT WIDTH
0
5
10
15
20
25
30
35
0 10 20 30 40 50 60 70 80 90 100 110 120
INCREMENT NUMBER
SPEC 1654

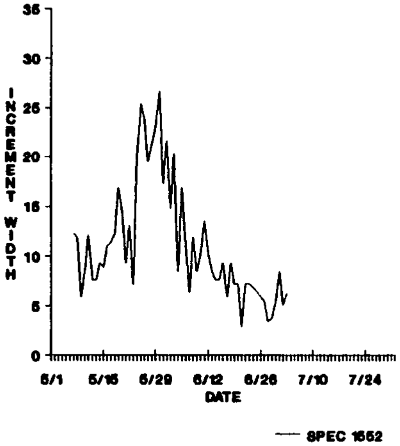

INCREMENT WIDTH
0
5
10
15
20
25
30
35
0 10 20 30 40 50 60 70 80 90 100 110 120
INCREMENT NUMBER
SPEC 1712

at various ages. However, there appeared to be consistent decreases in all otoliths between ages 3-10 and between 28-35 (arrows on Figures 4.16-4.19). Variations in hatching dates of individual fish may cause the mismatch of other periods of decreasing increment widths. Therefore, hatching dates for each individual fish were back-calculated by subtracting the age of the fish from the collection date (Table 4.4). No attempt was made to correct for the delay in first increment deposition. Several periods of coinciding decreases in increment widths were observed, with a decrease of 50% or greater between successive increments designated as a stress mark (Figures 4.20-4.23). Table 4.11 lists the dates of decreasing widths, the number of fish hatched and surviving during that period, the number of fish exhibiting a stress mark during that period, and the percentage of fish exhibiting the stress mark. In all periods identified, 50% or greater of the fish showed a stress mark. During the period May 13-15, 7 of the 13 fish exhibiting a stress mark (54%) showed that mark on 15 May, while during the period May 21-23, 8 of the fish showing a stress mark (73%) exhibited this mark on 21 May. Only 7 periods of decreasing widths did not fit into this pattern. These may have been caused by the individual fish experiencing a minor local stress event.

Figure 4.20. Mean increment widths by date for 4 fish from the James River in 1987.


35
30
25
20
15
10
5
0
INCREMENT WIDTH
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1549


35
30
25
20
15
10
5
0
INCREMENT WIDTH
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1551


35
30
25
20
15
10
5
0
INCREMENT WIDTH
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1552

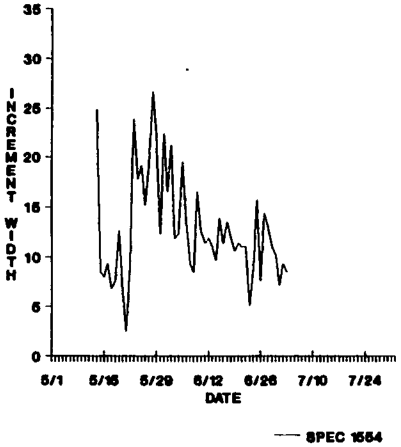
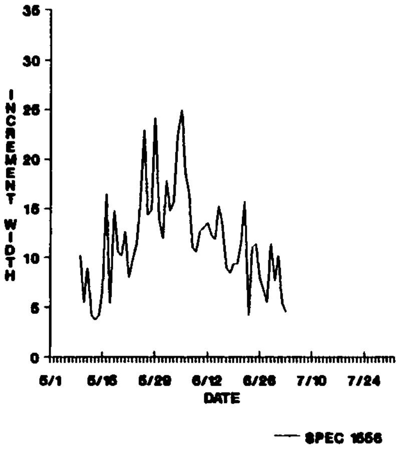
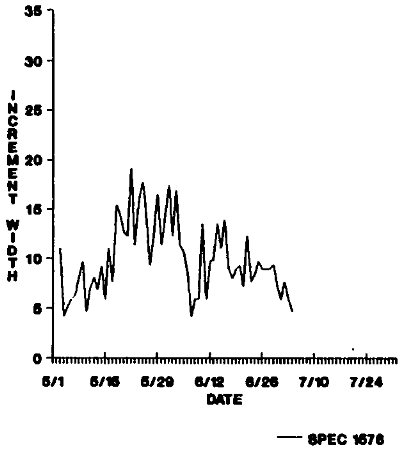
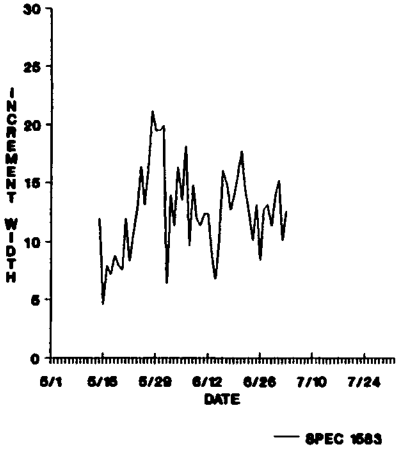

35
30
25
20
15
10
5
0
INCREMENT WIDTH
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1554

Figure 4.21. Mean increment widths by date for 4 fish from the James River in 1987.


INCREMENT WIDTH
0
5
10
15
20
25
30
35
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1556


INCREMENT WIDTH
0
5
10
15
20
25
30
35
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1576


INCREMENT WIDTH
0
5
10
15
20
25
30
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 1583

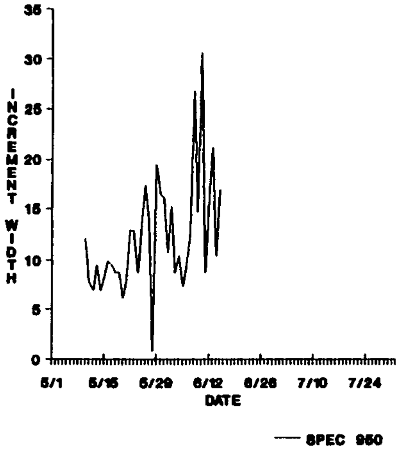
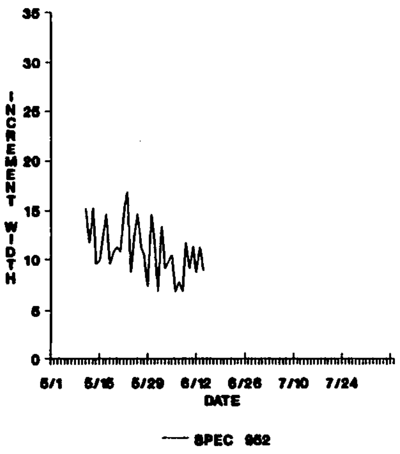
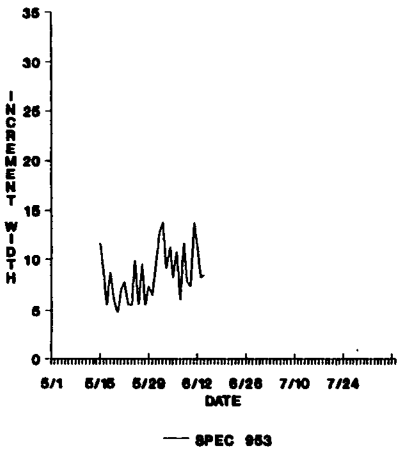
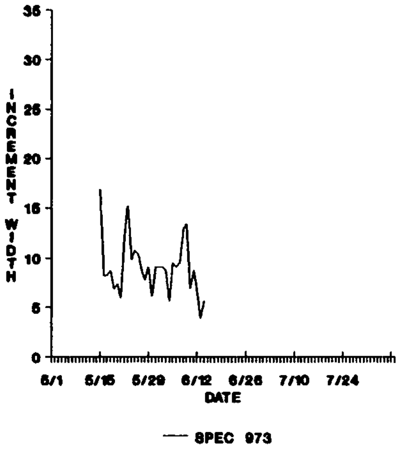
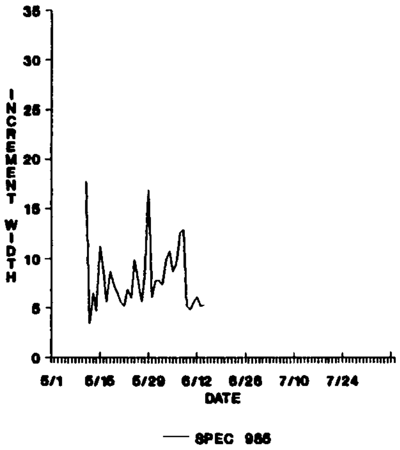

INCREMENT WIDTH
0
5
10
15
20
25
30
35
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 950

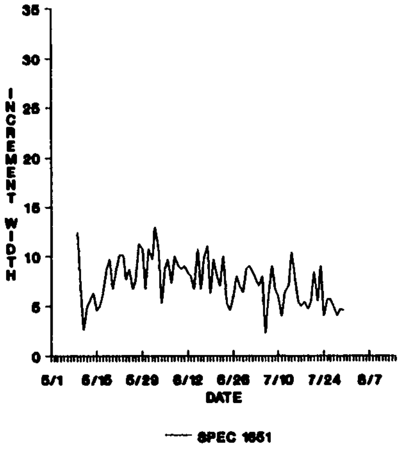
Figure 4.22. Mean increment widths by date for 4 fish from the James River in 1987.

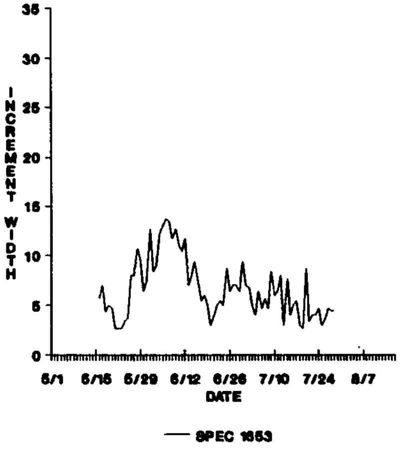

INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 952

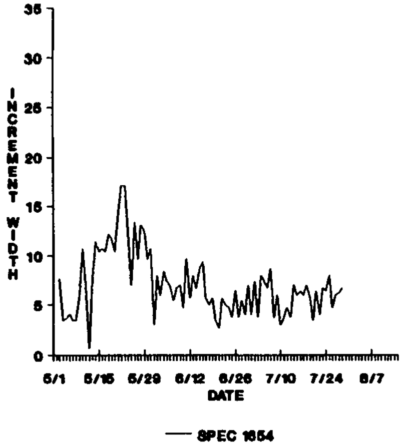

INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 953


INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 973


INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
DATE
SPEC 985


INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
8/7
DATE
SPEC 1651


INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
8/7
DATE
SPEC 1653


INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
8/7
DATE
SPEC 1654

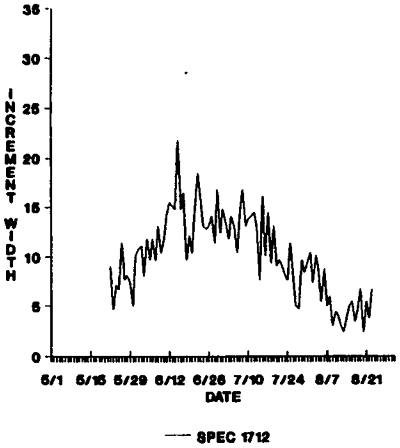

INCREMENT WIDTH
35
30
25
20
15
10
5
0
5/1
5/15
5/29
6/12
6/26
7/10
7/24
8/7
8/21
DATE
SPEC 1712

Table 4.11. Number of juvenile striped bass from the James River in 1987 showing a stress period in the form of decreasing otolith increment widths.

STRESS PERIOD	NO. FISH SURVIVING	NO. FISH W/ MARK	% FISH W/ MARK
MAY 01-03	3	2	67%
MAY 08-09	7	4	57%
MAY 13-15	16	13	54%
MAY 21-23	16	11	69%
MAY 29-31	16	10	63%
JUNE 04-08	16	8	50%
JUNE 11-14	12	8	67%
JUNE 18-21	11	7	64%
JULY 01-04	8	6	75%

DISCUSSION

Recent studies on the coupling between otolith and fish growth provide evidence that this relationship may be much more complex than previously thought. Secor and Dean (1989) suggested that population-specific otolith scaling patterns may exist within a single species. In the present study, the relationship between otolith and fish growth was not significantly different between populations. However, differences in the amount of variability in the population-specific relationships did exist. Coefficients of determination of the otolith-fish size relationships for separate populations varied from 0.11 to 0.76, with variations not being related to sample sizes, as was suggested by Secor et al. (1989). Variations also existed among hatchery-reared striped bass raised from the same brood stock under similar environmental conditions. Secor and Dean (1989) and Reznick et al. (1989) found a similar situation in pond-reared striped bass from South Carolina and genetically similar guppies raised under controlled laboratory conditions, respectively. They concluded that genetic and temporal factors can be discounted as influencing otolith scaling in these species.

The present study provides evidence that somatic growth rate differences among individual fish caused the high variability in the otolith-fish size relationships of juvenile striped bass populations. Somatic growth rate differences led to slower growing fish having larger otoliths at size than faster growing fish, as evidenced by the older hatchery-reared fish having an otolith 2-15% larger than a younger fish of similar size. A similar analysis involving pairs of wild striped bass of similar size showed that in approximately 80% of the cases the older slower growing fish had a larger otolith than the younger faster growing fish. These data provide evidence that as the differential between ages of fast and slow growing fish increases, a concurrent increase between the otolith radii will occur. Further evidence of the influence of somatic growth rates on the otolith-fish size relationships of juvenile striped bass was provided by the consistent increase in the coefficients of determination when fish were separated by 0.1 mm/day growth rate intervals. Volk et al. (1984) and Wilson and Larkin (1982) also suggested that otolith increment widths were effected by somatic growth rate differences.

Secor and Dean (1989) , Secor et al. (1989), and Reznick et al. (1989) also found that slower growing fish had larger otoliths than faster growing fish in striped bass and guppies, respectively. Reznick et al. (1989) found that inclusion of the residuals of otolith weight from the linear regression of otolith weight on fish length provided a better estimation of fish age. This was not tested in the present study, due to a lack of data on otolith weights. Reznick et al. (1989) suggested that slower growing fish tend to have positive residuals and faster growing fish tend to have negative residuals, as was verified in the present study. They also suggested that as fish grow, the otolith may undergo changes in shape due to differential deposition of calcium carbonate and that the measurement of otolith mass may be preferred over length. Secor and Dean (1989) found that inclusion of residuals did not increase the precision of age prediction for juvenile striped bass. In a more recent study, Secor et al. (1989) found that otolith length was a better predictor of age than fish length in wild striped bass populations, and suggested that greater variability existed in both somatic growth rates and the otolith-fish size relationship in field collected fish, as compared with pond-reared fish. The greater variability found in wild striped bass populations as compared to hatchery-reared fish in the present study supports these conclusions.

Penney and Evans (1985) and Neilson et al. (1985) found that slower growing year-classes had larger otoliths at size than fish collected during years of faster growth. The present study suggests that differences in otolith scaling patterns exist between year classes, as well as populations, of juvenile striped bass. Therefore, the otolith-fish size relationship must be verified on each separate year-class and population under study. Several authors have suggested an effect of varying environmental factors on otolith scaling. Secor et al. (1989), Campana (1984), and Marshall and Parker (1982) found feeding levels effected somatic growth of fish, thereby influencing the proportional rate of growth between the otolith and the fish. Secor et al. (1989) also found that varying cycles of feeding rates tended to cause otolith growth to become out of phase with somatic growth. Mosegaard et al. (1989), Savoy and Crecco (1987), and Campana (1984) suggested that temperature effects may also cause an uncoupling between otolith and fish growth. Campana (1984) and Savoy and Crecco (1987) suggested a direct effect of temperature on somatic growth, while Mosegaard et al. (1989) suggested an indirect effect of temperature on some metabolic activity controlling the deposition of daily increments on fish otoliths. Gutierrez and Morales-Nin (1986) suggested that otolith growth is a conservative process involving both the memory of previous growth and environmental conditions. They also found that temperature was the major factor influencing otolith growth and suggested that the effect of temperature may be on fish physiology and metabolism. Further research is needed to elucidate the exact relationship between otolith growth, somatic growth, and the effects of environmental factors on both these processes. Laboratory experiments on individually marked fish raised under controlled conditions and sequentially sampled are needed to provide further understanding of the relationship between otolith and fish growth.

Secor and Dean (1989), citing Campana and Neilson (1985), proposed a model to explain the uncoupling between otolith and fish growth by considering both the duration and the amplitude of calcium carbonate deposition. Their daily increment packing model predicts that a minimum amount of calcium carbonate will be deposited on the otolith in the form of a daily growth increment, whether the fish is growing or not. At faster growth rates an additional amount of calcium carbonate will be deposited on the otolith in addition to the minimum already deposited. Therefore, as somatic growth rates of individual fish diverge, the otoliths of the slower growing fish may eventually reach a larger size than the otoliths of the faster growing fish, even though the fish are equal in standard length. Results of the present study support the DIP model proposed by Secor and Dean (1989) by providing evidence that somatic growth rate differences among individual fish tend to cause large variations in the otolith-fish size relationships of juvenile striped bass, and that this variation is caused by slower growing fish having larger otoliths than faster growing fish.

The central assumption of the back-calculation technique is that a consistent, well-defined relationship exists between growth of any specific hard part and growth of the fish (Francis 1990; and Ricker 1976). The present study has shown that the otolith-fish length relationship is not consistent among all juvenile striped bass populations. Due to the large variability in the majority of relationships among the populations studied, it was felt that the back-calculation technique could be reliably applied only to the James River in 1987, which had a determination coefficient of 0.76.

Growth rates calculated for fish from the James River in 1987 reached a maximum of 0.690 mm/day at day 21-28 and later declined to 0.161 mm/day at day 98. Growth rates in %/day decreased from 9.5 to 0.4% for the 98 day period studied. A maximum length of 46.9 mm was reached in 98 days. Studies by Uphoff (1989), Houde and Lubber (1986), and Dey (1981) documented growth rates of 0.37-0.56 mm/day, 0.28-0.36 mm/day, and 0.1-0.2 mm/day, respectively, for larval striped bass (<appr. 15 mm). These growth rates are lower than those back-calculated from otolith increment widths in the present study. Growth rates calculated for juvenile striped bass have ranged from 0.272-0.433 mm/day (Trent 1962), 0.45 mm/day (Rathjen and Miller 1957) and 0.8-0.9 mm/day (Dey 1981). The back-calculation of growth rates for life stages was based on the otolith-fish length relationship calculated for juvenile striped bass between approximately 40 and 100 days of age. The extrapolation of this relationship to larval periods may

not be reliable if a shift in the relationship occurred at metamorphosis.

The growth rate calculated for the entire 98 day period was estimated at 0.421 mm/day, which corresponds to the estimated growth rate of 0.417 mm/day calculated from the standard length-estimated age regression (Chapter III). It appears that growth rates calculated for short periods of time (one week intervals) may be unreliable, while rates calculated for at least 98 days provide a very good estimate of population growth rates. Bradford and Geen (1987) found that growth rates calculated from otolith increment widths did not correspond to known growth histories over short time intervals. However, when longer time periods were considered, significant relationships were found.

The correspondence of standard lengths-at-capture and the Gompertz growth curve for fish between 30 and 50 days of age suggests that the back-calculation technique may be valid for these intermediate ages. The back-calculation of the Gompertz equation for all data, as well as when separated into weekly birthdate groupings, appeared to accurately estimate the lower range of lengths of fish greater than 50 days of age. The greater variability in lengths-at-capture of fish older than 50 days of age confounds the interpretation of the reliability of the Gompertz growth equation as a measure of growth of these fish.

An apparent 'reverse' Lee's phenomenon was observed in the James River in 1987, as indicated by the greater lengths-at-age back-calculated from older fish. There is considerable evidence that 'reverse' Lee's phenomenon does occur in the early life history of many fish species. During the first year of life, slower growing individuals are more susceptible to size-selective predation for a longer period of time (Cushing and Harris 1973; and Ware 1975). However, in the present study, this phenomenon may very well be an artifact of the small sample sizes used in this analysis, with only 2 fish between 60 and 70 mm and 4 fish between 20 and 30 mm. Ricker (1969) pointed out that biased sampling may cause Lee's phenomenon due to the efficiency of the sampling gear or a change in distribution or habits of older fish. The catch curve analysis presented in Chapter III provided evidence that juvenile striped bass were recruited to the sampling gear up to 70 mm standard length; however, at lengths greater than 90 mm juvenile striped bass appear to be not fully recruited to the sampling gear. There also appeared to be no emigration of juvenile striped bass less than 70 mm standard length in any of the river populations studied (Chapter III). In the present study, the small sample sizes were caused by the inclusion of those few otoliths which provided a straight transect from the primordium to the edge of the otolith. Larger sample sizes in future studies may provide more definitive conclusions on the occurrence of size-selective mortality on juvenile striped bass populations.

Victor (1982) provided evidence that the widths of otolith growth increments may provide a record of past stress events experienced by a fish. The plots of increment width by increment number presented in the present study show that the majority of fish studied appeared to show periodic decreases in increment widths through time. A decrease occurred in all fish at approximately 3-10 days, which may correspond to the time of first feeding of striped bass larvae (Albrecht 1964; Eldridge et al. 1977; and Rogers et al. 1977). A second stress mark observed in all fish studied appeared at approximately 30 days, which may indicate the metamorphosis from the larval to the juvenile stage. A similar decrease in increment widths occurred in all laboratory-reared striped bass at approximately 30 days of age (Chapter II). However, this mark was accompanied by a distinct opaque zone on all otoliths, which was not observed in any of the otoliths of the field-collected fish. It appears possible that the decrease in somatic growth of the fish at 30 days, combined with the stress of shipping and handling, may have amplified the normal decrease in increment widths occurring at 30 days of age in these fish. The correspondence of rapid decreases in increment widths when plotted by date rather than increment number of individual fish, suggests that fish may be experiencing similar stress periods in nature. No exact cause of these apparent stress marks on individual otoliths can be provided. However, it may be assumed that they indicate periods of declining environmental quality, switch of prey items, or migrations into less favorable environments. Further research is required to provide a better understanding of the link between stress periods and otolith increment widths. If a relationship can be demonstrated, the evaluation of otolith increment widths of field-collected striped bass, in conjunction with environmental data, may provide a greater understanding of the dynamics of fish growth and survival.

This study provides evidence in support of recent research indicating that the relationship between otolith and fish growth may be population-, as well as species-specific. The otolith-fish size relationship must, therefore, be validated for separate populations, due to the great variability in the relationship between populations. Populations consisting of individual fish growing at variable somatic growth rates may contain so much variability that the back-calculation of length-at-age for that population may be invalid. Future research needs to elucidate the effects of variable somatic growth rates on the otolith-fish length relationship and the applicability of the back-calculation technique to such populations.

GENERAL DISCUSSION

The present study has shown a consistent underestimation of ages of older striped bass (>80 days old) using the otolith aging technique. Other published studies have also shown an underestimation of ages of older fish of other species (Jones and Brothers 1987; Tsukamoto and Kajihara 1987; Marshall and Parker 1982; Neilson and Geen 1982; Taubert and Coble 1977). Several possible causes of this underestimation have been hypothesized: 1) cessation of daily increment deposition due to decreasing water temperatures (Marshall and Parker 1982; and Taubert and Coble 1977) or periods of starvation (Jones and Brothers 1987), 2) resolution problems of narrow increments with the light microscope (Jones and Brothers 1987; and Campana and Neilson 1985), and 3) inappropriate grinding and enumeration techniques (Campana and Neilson 1985). The present study does not provide insights into the causes of underestimation in juvenile striped bass. The relationship between mean increment counts and known age for hatchery-reared juvenile striped bass appears to be non-linear, but constantly positive, after 80 days. The present study suggests that a correction factor can be calculated to adjust for the underestimation of ages of older striped bass up to

110 days, after which variation becomes too high to allow a correction to be accurately applied. Daily deposition of growth increments on otoliths of other species must be conscientiously validated before application of the otolith aging technique.

It has been suggested by several authors that the measurement of otolith increment widths can provide a method of reconstructing the growth history of individual fish. For this method to be valid, a consistent relationship must be shown to exist between somatic growth of the fish and growth of the otolith. The present study provides evidence that there is an uncoupling of the otolith radius-fish length relationship during periods of slow somatic growth. The laboratory experiments performed under constant photoperiod conditions, and the data on hatchery-reared and field-collected juvenile striped bass, showed that slower growing striped bass had larger otoliths than the faster growing fish of similar size. Chapter III also provided evidence that population-specific otolith scaling patterns exist in wild striped bass populations. This study showed that somatic growth rate differences among individual fish caused increased variability in the otolith-fish size relationships of juvenile striped bass populations. An uncoupling between somatic fish growth and growth of the otolith has been shown to exist in other species (Mosegaard et al. 1989; Secor and Dean 1989; Secor et al. 1989; Savoy and Crecco 1987; Neilson et al. 1985;

Penney and Evans 1985; Campana 1984; Volk et al. 1984; and Wilson and Larkin 1982). Due to the varying results concerning the relationship between somatic fish growth, otolith growth, and the effects of environmental factors on both these processes, an otolith-fish size relationship must be verified on a population-specific basis before attempting to reconstruct individual growth histories through the measurement of increment widths.

Data provided by the laboratory experiments (Chapter II) and the application of the back-calculation technique to the James River in 1987, which showed the best relationship between otolith radius and standard length (Chapter IV), provided evidence that the back-calculation technique may be valid in reconstructing an average growth history of juvenile striped bass for periods of time longer than on a daily basis. These results are in direct opposition of the conclusions of Gutierrez and Morales-Nin (1986), who suggested that otolith growth is a conservative process involving both the memory of pervious growth and environmental conditions, and that otolith increment widths could only be applied to back-calculating average growth histories of individual fish.

The otolith aging technique appears to be a valid method of calculating population- and cohort-specific estimates of growth and mortality (Chapter III). The calculation of population-specific estimates of mortality suggests that juvenile striped bass are fully recruited to the sampling gear at approximately 60 days of age and are not fully recruited to the gear after about 90 days. Analysis of length-frequencies for each river population by collection dates also suggests that juvenile striped bass may be emigrating out of the rivers by the beginning of September. The juvenile striped bass index, used to provide management regulations for the Atlantic Coast striped bass fishery, is calculated from the collection of juvenile striped bass using the same sampling gear as was utilized in the present study. The data on gear selectivity and emigration provided by this study may be useful in limiting the juvenile striped bass survey to the period when fish are fully recruited to the sampling gear, thereby providing better estimates of relative abundance.

The calculation of cohort-specific estimates of growth and mortality was limited by the small sample sizes used in the analysis. Larger sample sizes than those used in the present study would increase the reliability of these estimates. The major limiting factor to larger sample sizes in this study was the amount of time required to process the otoliths for analysis (Appendix B). An analysis of cohort-specific estimates of mortality, based on larger sample sizes, could provide the period of time when mortality of juvenile striped bass becomes stable. This data, combined with the data on gear selectivity and emigration, could suggest a short period of time when year-class strength of juvenile striped bass is set. This data could have major implications for the amount of time and money presently invested in accurately determining relative abundance of juvenile striped bass populations.

Environmental factors affecting year-class strength of juvenile striped bass populations could not be determined in the present study. In future studies, a comparison of spawning stock distributions, the back-calculated birthdate distributions, and environmental factors during spawning may lead to an understanding of the factors causing critical periods of survival during the early life stages of this species. The integration of cohort-specific estimates of growth and mortality, and environmental factors, could also lead to increased knowledge of the factors influencing recruitment and year-class strength of juvenile striped bass populations.

Analyses in the present study showed a great deal of variability in the relationships between standard length and age, otolith radius and standard length, and the estimates of mortality, growth, stomach fullness, and CPUE. Growth rate and mortality estimates of juvenile striped bass through time were also extremely variable. These data suggest that the relationships between these factors are non-linear. However, due to the inherent variability in the standard length-age and otolith-fish size relationships, a non-linear analysis did not provide a better fit than the linear analyses. Further growth rate and mortality estimates of juvenile striped bass populations are needed to elucidate the possibility that the relationships are non-linear. Until further estimates are available, no conclusions can be made on the influence of density-independent and density-dependent factors on year-class strength and mechanisms of recruitment in juvenile striped bass populations.

Appendix A

Summary data on field-collected juvenile striped bass

Summary data of field collected young-of-the-year striped bass in the James River in 1986 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
03 July	36	4	30.1-42.6	3	60.0
	1	24	33.3-71.6	12	71.6
	3.5	1	29.2	1	82.0
15 July	27	1	65.0	0	---
	36	38	32.0-46.2	13	75.0
	1	14	30.7-63.5	2	91.0
	3	32	38.9-79.6	0	---
	46	38	32.5-74.9	12	74.8
	57	35	35.9-67.1	8	77.9
23 July	46	2	59.9-75.3	2	50.0
	50	4	47.2-52.4	3	94.0
	54	2	43.8-50.3	0	---
	58	9	39.3-73.5	0	---
07 August	27	4	63.5-85.4	3	104.3
	36	9	48.7-72.2	0	---
	1	5	48.3-52.5	0	---
	3	18	53.7-91.0	6	110.2
	43	6	40.5-65.0	0	---
	57	43	44.1-82.0	0	---

12 August	55	1	48.6	0	---
14 August	48	1	61.4	0	---
	51	3	61.2-87.5	0	---
	53	3	64.6-79.6	3	108.5
	54	8	45.5-68.3	0	---
	58	6	51.9-73.4	3	106.5
21 August	55	10	49.2-89.5	5	90.3
	59	12	47.1-60.4	4	106.5
23 August	54	44	42.7-88.5	11	101.5
	56	6	49.8-76.2	0	---
26 August	27	4	75.0-80.7	0	---
	36	13	62.8-87.6	6	107.8
	1	8	52.2-65.5		
	3	8	62.9-112.3	4	98.0
	46	27	45.4-84.8	12	102.3
	57	16	45.7-60.1	0	---
03 Sept	40	5	50.7-69.5	3	125.5
	42	7	57.7-73.8	3	136.2
	46	5	54.5-64.9	2	114.3
10 Sept	42	3	50.5-50.9	0	---
	43	11	45.3-86.7	8	146.4
	49	1	56.6	0	---
	50	8	49.1-69.2	6	160.5

22 Sept	27	2	81.3-82.0	0	---
	36	3	62.4-64.6	0	---
	1	3	59.1-64.5	0	---
	3	2	72.9-74.2	0	---
	46	3	74.5-80.2	0	---
	57	5	48.9-64.9	0	---
29 Sept	27	3	83.4-93.0	0	---
	39	2	80.7-91.5	0	---
	46	13	53.1-80.6	0	---
TOTALS		502		135	

Summary data of field collected young-of-the-year striped bass from the Mattaponi River in 1986 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
07 July	44	1	96.9	0	---
14 July	45	1	38.5	0	---
17 July	33	5	35.4-60.8	2	79.5
	41	13	36.5-120.7	6	81.2
	44	8	34.8-44.7	0	---
	47	3	39.6-46.6	0	---
06 August	33	2	59.6-61.9	0	---
	41	6	49.8-105.2	2	102.5
	44	8	45.3-50.7	1	100.0
	47	3	40.0-42.9	0	---
29 August	33	1	110.7	0	---
	41	4	60.6-71.2	0	---
	47	7	65.7-129.1	0	---
19 Sept	33	3	74.7-81.5	0	---
	41	4	66.8-73.7	0	---
	47	1	68.1	0	---
TOTALS		70		11	

Summary data of field collected young-of-the-year striped bass from the Pamunkey River in 1986 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
26 June	51	39	33.2-123.1	9	68.4
11 July	44	3	35.2-43.9	0	---
	51	29	25.0-58.8	4	---
16 July	41	4	34.5-48.1	1	89.0
05 August	41	2	55.3-58.3	0	---
	51	4	48.6-72.8	2	95.5
19 August	41	1	46.5	0	---
	43	31	48.2-74.7	0	---
27 August	44	4	57.1-65.1	0	---
	51	5	49.1-69.4	0	---
18 Sept	42	1	80.6	0	---
	51	2	66.5-72.1	0	---
TOTALS		125		16	

Summary data of field collected young-of-the-year striped bass from the Rappahannock River in 1986 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
14 July	44	4	39.2-45.2	0	---
	50	47	28.6-45.1	25	85.7
	55	65	33.4-44.9	16	89.5
04 August	50	20	39.2-50.6	9	98.4
	55	33	37.1-51.0	15	100.3
20 August	53	5	52.7-58.2	0	---
25 August	27	1	68.2	0	---
	50	15	43.4-60.1	10	109.8
	55	14	45.4-57.5	9	103.6
17 Sept	44	4	55.6-62.0	0	---
	50	1	45.6	0	---
	55	37	43.2-79.0	22	127.5
TOTALS		246		106	

Summary data of field collected young-of-the-year striped bass from the James River in 1987 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
18 June	1	23	16.6-29.2	6	54.2
	7	3	24.9-36.0	0	---
	46	1	19.6	0	---
	54	12	18.1-26.6	0	---
	55	8	16.1-30.2	0	---
07 July	60	3	40.0-52.6	0	---
	62	1	51.9	0	---
	68	4	36.5-52.9	0	---
	70	8	34.0-61.8	4	67.5
	72	2	37.8-54.2	0	---
	75	21	30.5-44.6	9	72.1
16 July	36	11	30.5-50.3	6	76.8
	1	33	28.8-58.8	14	80.4
	3	23	32.5-62.2	0	---
	46	31	28.9-41.2	5	79.2
	57	8	46.1-56.7	0	---

03 August	26	5	40.2-57.9	0	---
	36	32	38.2-59.5	8	86.5
	1	37	31.9-71.7	4	89.4
	46	30	34.2-42.6	6	92.3
24 August	59	16	47.2-69.9	8	103.6
	61	7	58.2-81.0	0	---
	71	2	54.5-61.2	0	---
	77	7	50.7-56.5	4	106.2
	79	18	46.7-58.5	2	109.5
28 August	27	7	52.6-74.2	0	---
	36	12	40.4-61.6	0	---
	1	30	35.6-98.7	0	---
	3	8	41.2-83.4	0	---
	46	35	35.1-66.0	6	107.9
	57	23	46.3-117.6	0	---
TOTALS		461		83	

Summary data of field collected young-of-the-year striped bass from the Mattaponi River in 1987 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
22 June	39	2	19.9-24.3	0	---
	43	17	15.8-23.8	5	56.5
	44	4	15.8-20.5	0	---
	46	3	14.2-24.6	0	---
	47	3	16.3-22.8	0	---
	49	1	17.0	0	---
	52	2	13.8-15.4	0	---
	54	1	17.6	0	---
23 June	39	1	17.6	0	---
	40	1	17.6	0	---
29 June	46	2	21.5-25.8	0	---
	50	6	18.9-34.5	0	---
	53	1	27.6	0	---
	54	1	17.9	0	---
30 June	39	3	20.8-26.9	0	---
	40	4	20.1-23.5	0	---
	41	2	20.9-21.9	0	---

06 July	48	1	23.8	0	---
08 July	41	19	29.3-68.7	14	67.7
	45	5	36.5-62.5	3	63.4
14 July	33	23	29.3-53.5	13	69.0
	40	4	24.5-46.4	3	68.3
	41	7	35.8-53.1	4	74.5
	44	1	27.7	0	---
	47	16	27.8-62.8	6	65.7
	50	1	24.1	0	---
	54	2	23.3-24.8	0	---
	57	1	34.6	0	---
20 July	39	1	29.2	0	---
	41	1	31.0	0	---
	50	1	24.1	0	---
28 July	41	1	67.1	0	---
04 August	29	4	40.4-53.0	0	---
	34	8	42.8-58.5	4	95.6
	41	4	40.7-43.2	0	---
	44	6	35.9-127.0	3	87.3
	47	8	35.9-50.4	2	92.8

26 August	33	28	38.1-71.4	19	100.3
	44	4	37.7-41.7	2	107.5
	47	4	43.0-75.6	0	---
TOTALS		202		78	

Summary data of field collected young-of-the-year striped bass from the Pamunkey River in 1987 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
11 June	47	1	14.5	0	---
	48	1	15.5	0	---
	58	1	27.6	0	---
19 June	38	6	18.3-22.2	4	56.8
	39	3	19.9-24.4	0	---
	40	3	20.5-22.7	0	---
	41	3	21.9-23.9	0	---
	45	4	19.7-23.7	0	---
	47	5	18.2-21.7	0	---
24 June	42	2	19.7-22.8	0	---
	45	5	17.3-27.2	0	---
	47	2	19.1-20.9	0	---
	52	3	14.8-25.6	0	---
	53	2	24.8-27.9	0	---
	54	7	12.4-27.6	0	---
30 June	53	1	28.8	0	---
01 July	37	2	19.9-24.9	0	---

07 July	55	1	28.3	0	---
	42	4	26.2-40.2	0	---
	44	3	35.5-57.5	0	---
	52	1	25.5	0	---
	55	2	27.7-29.8	0	---
10 July	40	1	40.8	0	---
	41	1	21.3	0	---
	43	1	37.2	0	---
	46	1	25.3	0	---
14 July	44	34	21.5-59.3	13	72.4
	51	22	33.2-64.5	11	76.9
	60	1	22.9	0	---
16 July	40	1	28.6	0	---
	42	6	24.9-34.7	0	---
	44	2	28.5-30.0	0	---
	46	1	26.3	0	---
20 July	47	3	24.7-27.4	0	---
	54	1	29.5	0	---
	58	2	33.5-39.3	0	---
22 July	42	1	31.9	0	---
	45	1	33.5	0	---
	48	1	25.8	0	---
27 July	49	7	32.1-50.6	3	87.9
	50	5	32.5-39.1	2	89.1
	55	8	39.3-45.5	3	84.3

04 August	35	28	39.8-60.3	10	97.5
	41	11	36.7-48.7	5	92.1
	44	27	34.4-57.9	12	95.7
	51	15	39.2-72.7	6	93.2
25 August	41	4	37.0-60.9	0	---
	44	15	35.3-75.1	3	110.3
	51	5	49.6-81.8	0	---
TOTALS		296			72

Summary data of field collected young-of-the-year striped bass from the Rappahannock River in 1987 by date and station. Length range is recorded as the standard length (mm).

DATE	STATION	TOTAL COLLECTED	LENGTH RANGE	TOTAL AGED	MEAN AGE
19 June	50	26	11.7-23.3	5	50.3
	55	35	18.0-47.8	0	---
	62	12	12.6-29.6	0	---
	71	4	25.2-41.5	0	---
	73	10	18.2-33.9	0	---
13 July	28	5	34.9-53.2	0	---
	37	130	30.8-63.3	13	66.5
	44	31	27.8-68.1	7	59.3
	50	93	25.2-40.4	11	54.2
	55	49	27.6-38.7	0	---
31 July	44	45	31.8-47.6	0	---
	50	47	27.6-38.8	0	---
	55	67	27.5-71.3	7	71.4
01 August	28	8	48.9-64.3	0	---
	37	53	30.6-53.0	10	78.9

10 August	22	10	40.1-64.9	0	---
	50	8	34.5-36.2	0	---
	55	31	33.5-50.1	12	86.8
	57	3	43.9-47.2	0	---
	59	12	39.9-102.4	0	---
	62	1	43.7	0	---
	65	1	45.5	0	---
	69	5	42.0-55.3	0	---
	77	1	45.4	0	---
	80	2	41.4-41.6	0	---
27 August	37	26	39.9-68.2	10	100.3
	50	27	35.7-68.0	7	109.4
	55	51	34.5-91.5	15	107.8
TOTALS		793		87	

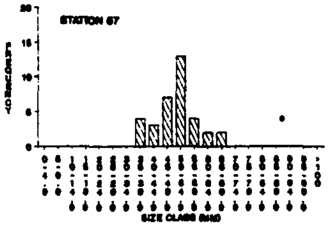
Appendix B

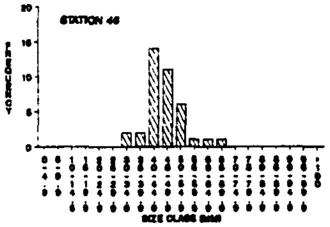
Length-frequencies by 2-week collection dates for each river population studied

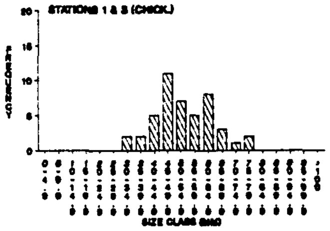
JULY 15

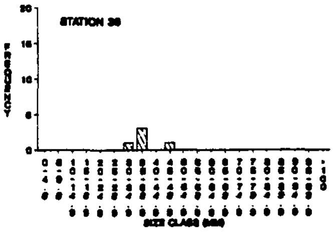
JAMES RIVER 1986

UPRIVER

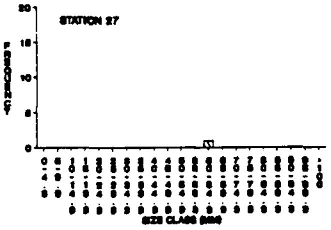








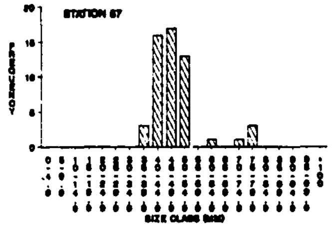
DOWNRIVER

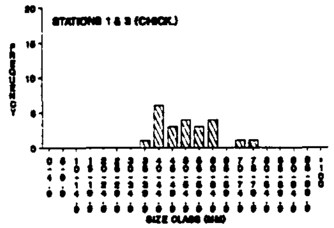


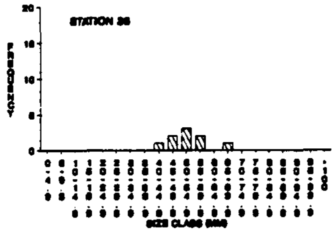
AUGUST 07

JAMES RIVER 1986

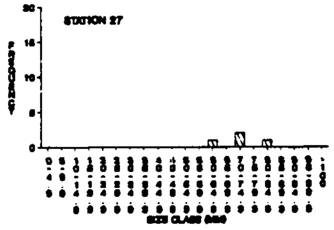
UPRIVER







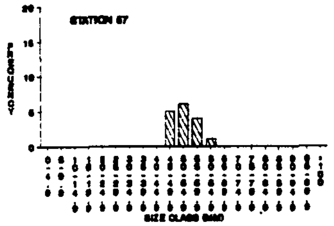
DOWNRIVER

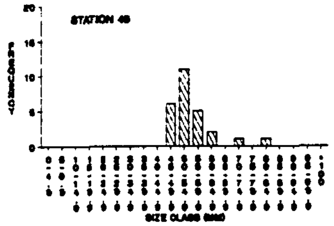


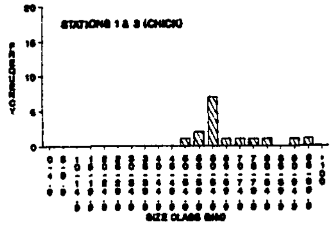
JAMES RIVER 1986

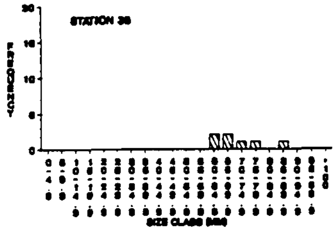
AUGUST 26

UPRIVER

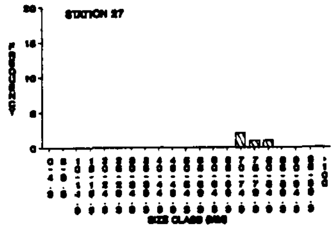






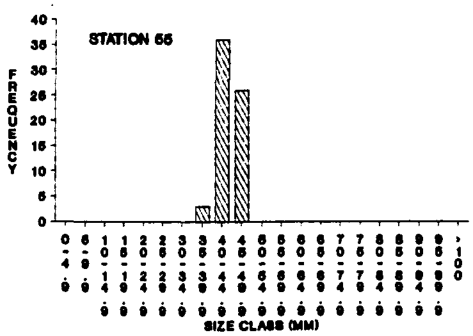


DOWNRIVER

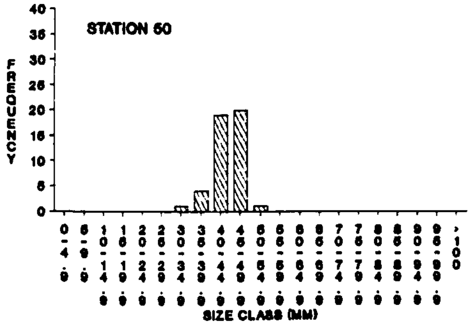


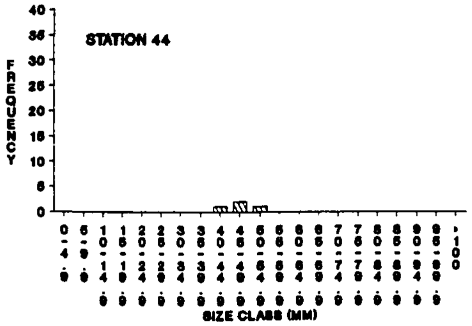
RAPPAHANNOCK RIVER 1986

JULY 14



UPRIVER



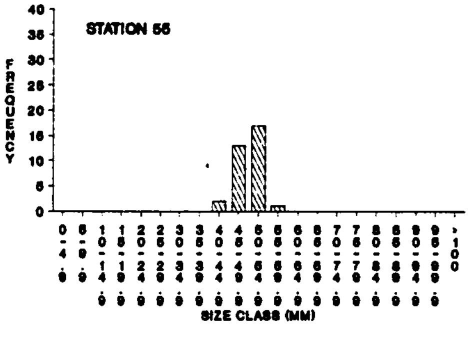


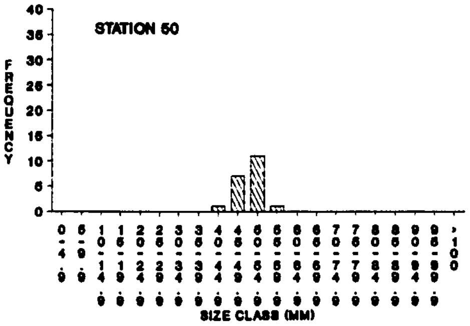
DOWNRIVER

AUGUST 4

RAPPAHANNOCK RIVER 1986

UPRIVER



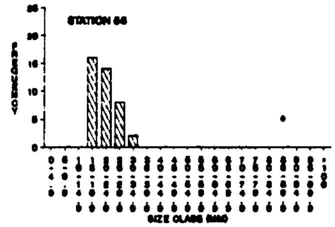


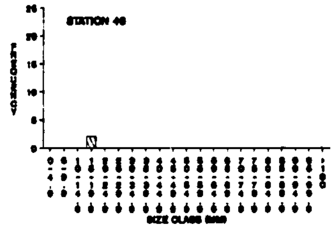
DOWNRIVER

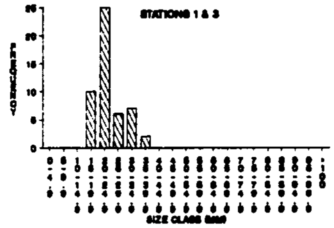
JAMES RIVER 1987

JUNE 18

UPRIVER





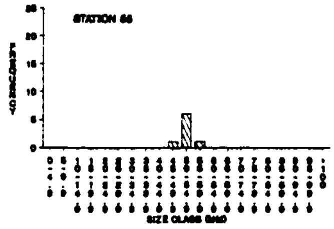


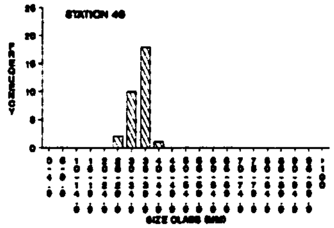
DOWNRIVER

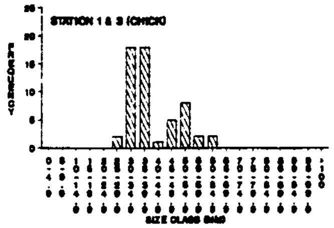
JAMES RIVER 1987

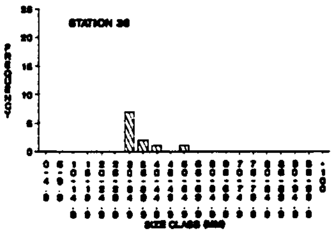
JULY 16

UPRIVER







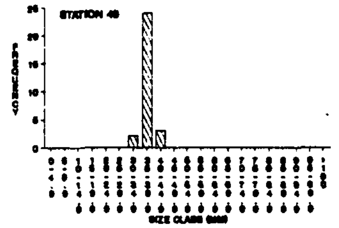


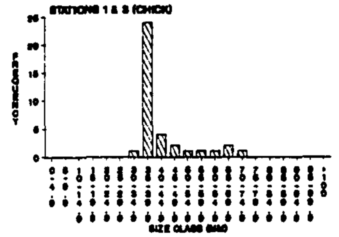
DOWNRIVER

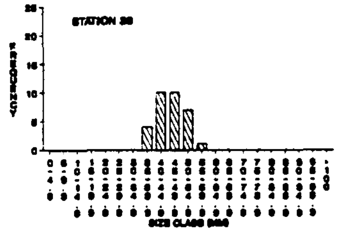
JAMES RIVER 1987

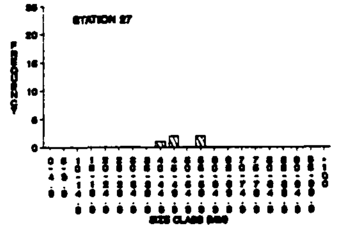
AUGUST 3

UPRIVER







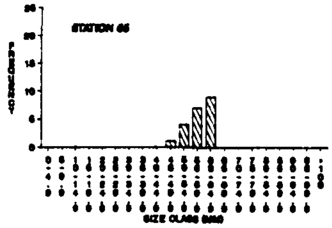


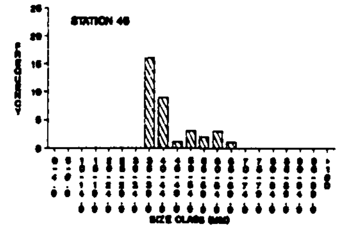
DOWNRIVER

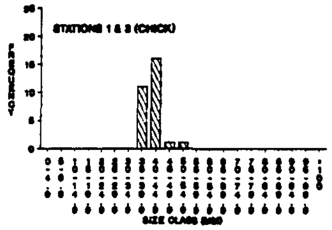
JAMES RIVER 1987

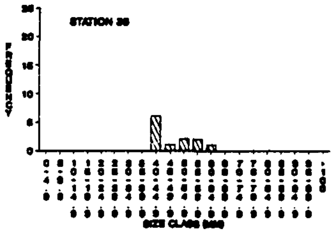
AUGUST 28

UPRIVER

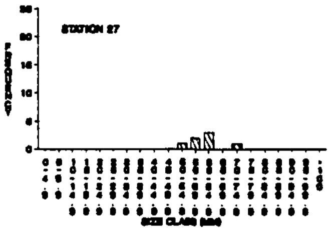








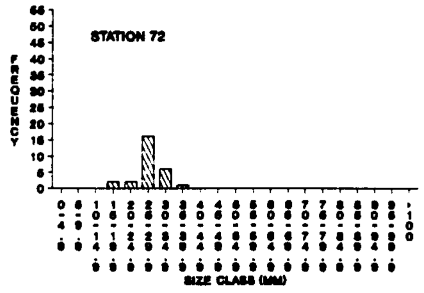
DOWNRIVER

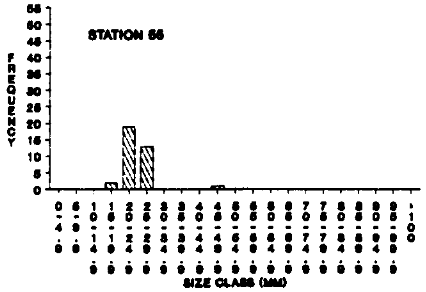


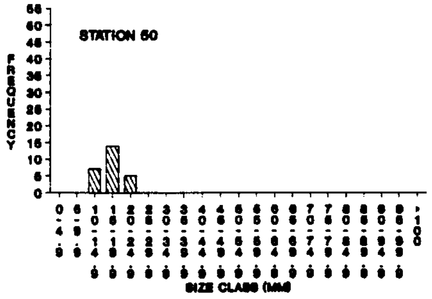
RAPPAHANNOCK RIVER 1987

JUNE 19

UPRIVER





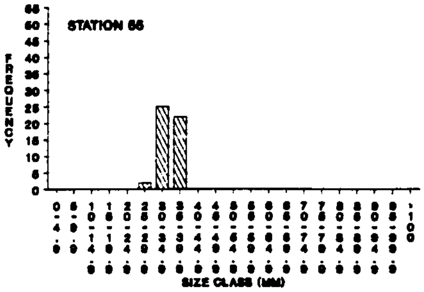


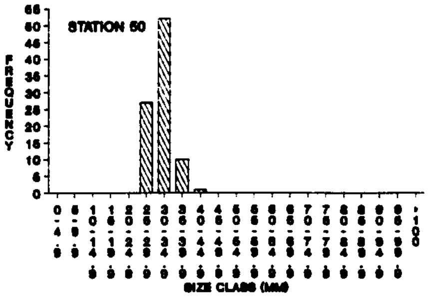
DOWNRIVER

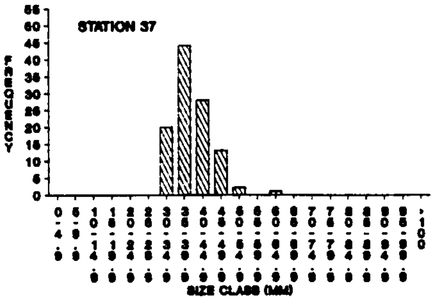
RAPPAHANNOCK RIVER 1987

JULY 13

UPRIVER





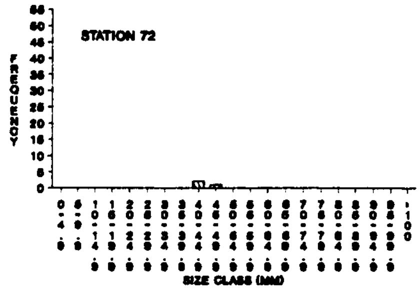


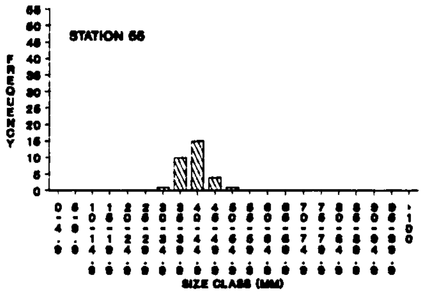
DOWNRIVER

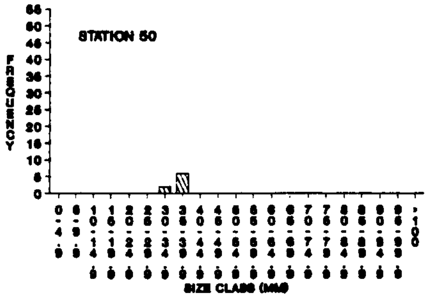
RAPPAHANNOCK RIVER 1987

AUGUST 10

UPRIVER





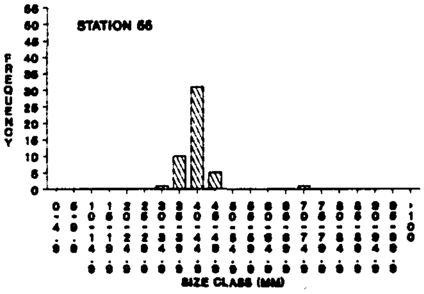


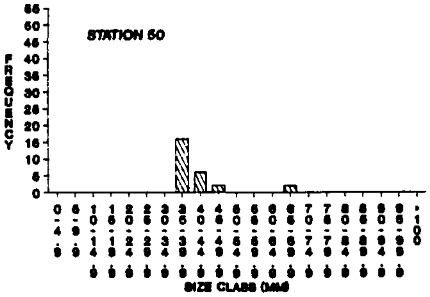
DOWNRIVER

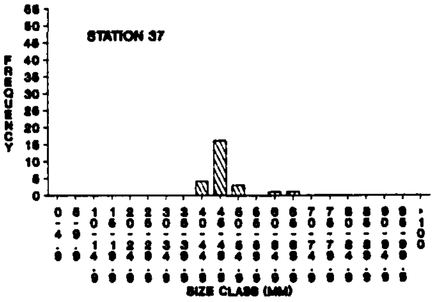
RAPPAHANNOCK RIVER 1987

AUGUST 27

UPRIVER





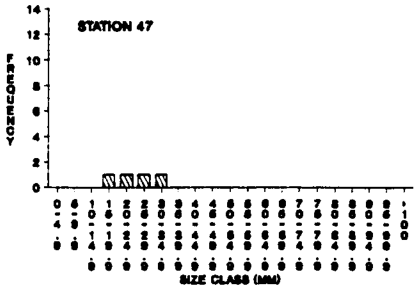


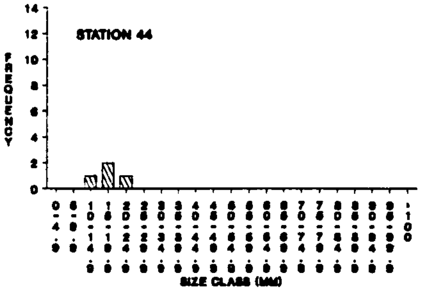
DOWNRIVER

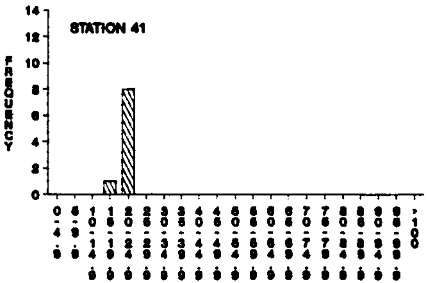
MATTAPONI 1987

JUNE 30

UPRIVER





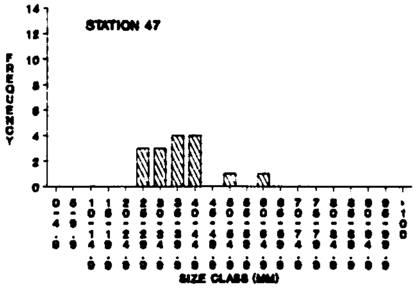


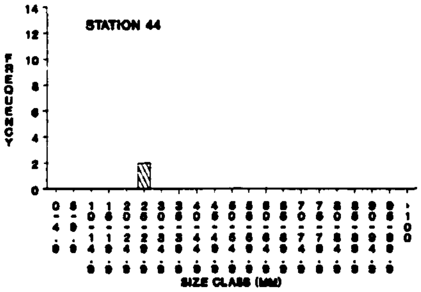
DOWNRIVER

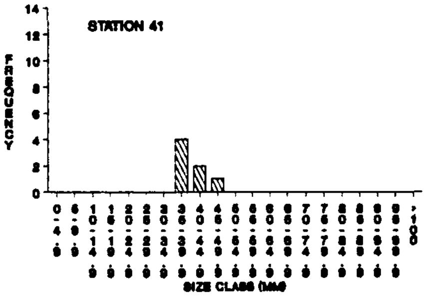
MATTAPONI 1987

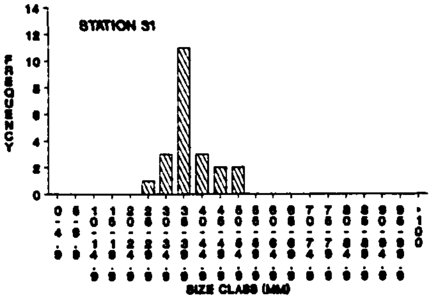
JULY 14

UPRIVER







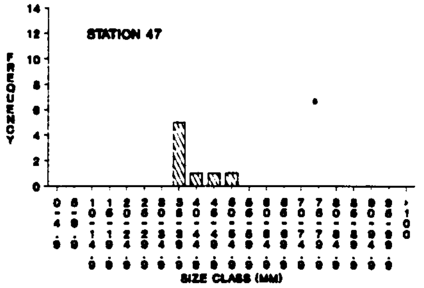


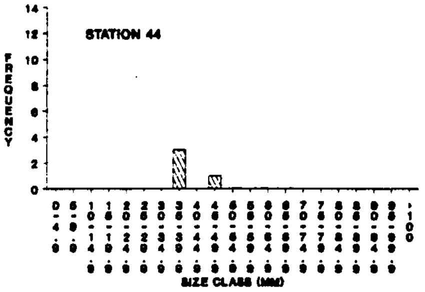
DOWNRIVER

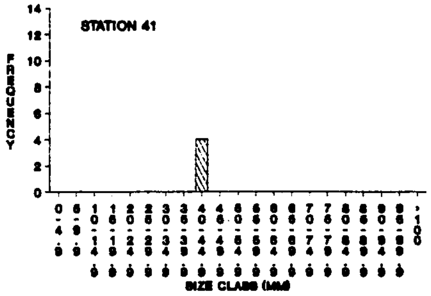
MATTAPONI 1987

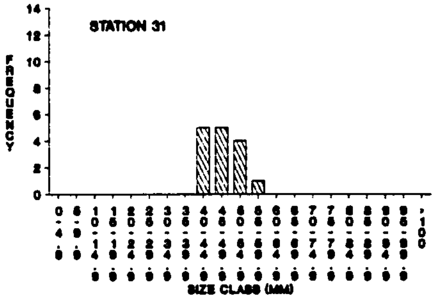
AUGUST 4

UPRIVER







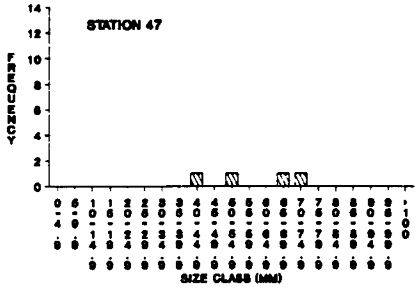


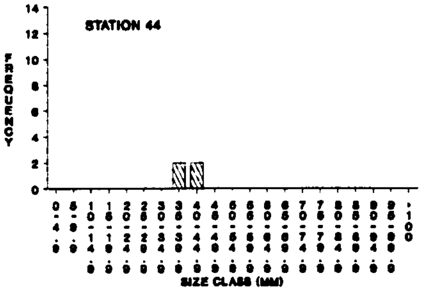
DOWNRIVER

MATTAPONI 1987

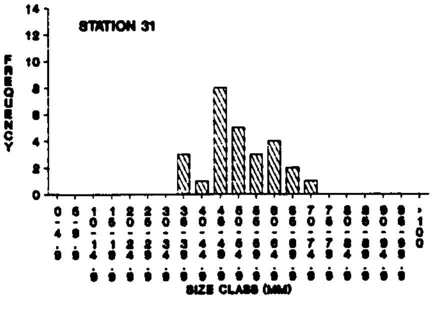
AUGUST 26

UPRIVER





DOWNRIVER



Appendix C

Otolith preparation methods

I. FISH PROCESSING & OTOLITH REMOVAL

1. Length and weight measurements
2. Removal of sagittal otoliths

Time = appr. 25 fish/hour

II. EMBEDDING OF SAGITTAL OTOLITHS

1. Fill Pelco embedding molds halfway with Spurr medium and heat at appr. 80 degrees for 24 hours.
2. Place sagittal otoliths longitudinally in molds, fill completely with Spurr medium, and heat at 80 degrees for 24 hours. (20 sagitta/Pelco embedding tray)

III. TRANSVERSE CUTTING OF SAGITTA

1. Place the embedded otolith in the Buehler isomet saw chuck, and cut transversely on either side of the sagitta.

Time = appr. 20 sagitta/hour

IV. GRINDING OF SAGITTA

1. Attach Spurr block containing sagitta onto a microscope slide with Crystalbond.
2. Grind sagitta until the section is near the primordium. (Constant checking under dissecting microscope)
3. Melt Crystalbond and flip otolith section.
4. Grind sagitta from the other side until the primordium is at the surface. Section thickness should be appr. 10 um. (Constant checking under compound microscope)

Time = appr. 20 min./otolith

V. ENUMERATION OF GROWTH INCREMENTS

1. Count growth increments under compound microscope

Time = appr. 10 min./otolith (with the BIOSONICS OPRS)
= appr. 20 min./otolith (w/out the BIOSONICS OPRS)

LITERATURE CITED

Albrecht, A. B. 1964. Some observations on factors associated with survival of striped bass eggs and larvae. Calif. Fish and Game 50:100-113.

Aschoff, J., S. Daan, and G. A. Goos (ed.). 1982. Vertebrate Circadian Systems. Springer-Verlag, N. Y.

Atlantic States Marine Fisheries Commission. 1981. Interstate fisheries management plan for the striped bass of the Atlantic Coast - Maine to North Carolina.

Austin, H.M. 1980. Biology of adult striped bass, *Morone saxatilis*. Pages 123-131. *In* Clepper (ed.). Proceedings of the Fifth Annual Marine Recreational Fisheries Symposium Sport Fishing Institute, Washington, D.C.

Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101-136. *In* T. B. Bagenal (ed). Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, England.

Barkman, R. C., and D. A. Bengston. 1987. The record of daily growth in otoliths of Atlantic silversides, *Menidia*, from field and laboratory. J. Fish Biol. 31:683-695.

Bennett, M. F. 1974. Living Clocks in the Animal World. C. C. Thomas, publisher. Springfield, Ill.

Berggren, R. J., and J. T. Lieberman. 1978. Relative contribution of Hudson, Chesapeake, and Roanoke striped bass, *Morone saxatilis*, stocks to the Atlantic coast fishery. U. S. Fish. Wildl. Serv. Fish. Bull. 76:335-345.

Boreman, J., and H. M. Austin. 1985. Production and harvest of anadromous striped bass stocks along the Atlantic coast. Trans. Am. Fish. Soc. 114:3-7.

Bosclair, D., and W. C. Leggett. 1989. Among-population variability of fish growth: III. Influence of fish community. Can. J. of Fish. Aquat. Sci. 46(9):1539-1550.

Bradford, M. J., and G. H. Geen. 1987. Size and growth of juvenile chinook salmon back-calculated from otolith growth increments. Pages 453-462. In R. C. Summerfelt and G. E. Hall (ed.). Age and Growth of Fish. Iowa State University Press, Ames, Iowa.

Brady, J. 1979. Biological Clocks. University Park Press, Baltimore, MD.

Brothers, E. B. 1981. What can otolith microstructure tell us about daily and subdaily events in the early life history of fish? Rapp. P.-v. Reun. Cons. Int. Explor. Mer 178:393-394.

Brothers, E. B. 1984. Otolith studies on early life history stages of fishes: applications to systematics. In G. Moser (ed.). Ontogeny and systematics of fishes.

Brothers, E. B., and McFarland. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited grunts (Haemulons flavolineatum Desmarest: Haemulidae). Rapp. P.-v. Cons. int. Explor. Mer 178:369-374.

Brothers, E. B., E. D. Prince, and D. W. Lee. 1983. Age and growth of young-of-the-year bluefin tuna from otolith microstructure. Nat. Mar. Fish. Serv. Tech. Rep. No. 8.

Brothers, E. B., C. P. Mathews, and R. Lasker. 1976. Daily growth increments in otoliths from larval and adult fishes. U. S. Fish Wildl. Serv. Fish. Bull. 74:1-8.

Bunning, E. 1973. The Physiological Clock: Circadian Rhythms and Biological Chronometry. The English Universities Press Ltd., London.

Campana, S. E. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014-1032.

Campana, S. E. 1984A. Lunar cycles of otolith growth in the juvenile starry flounder, Platichthys stellatus. Mar. Biol. 80:239-246.

Campana, S. E. 1984B. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder. Can. J. Zool. 62:1507-1512.

Campana, S. E. 1983. Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout and starry flounder. Can. J. Zool. 61(7):1591-1597.

Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014-1032.

Campana, S. E., and J. D. Neilson. 1982. Daily growth increments in otoliths of starry flounder (Platichthys stellatus) and the influence of some environmental variables in their production. Can. J. Fish. Aquat. Sci. 39(7):937-942.

Cech, J. J., Jr., S. J. Mitchell, and T. E. Wragg. 1984. Comparative growth of juvenile white sturgeon and striped bass: Effects of temperature and hypoxia. Estuaries 7(1):12-18.

Chapoton, R. B., and J. E. Sykes. 1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. Trans. Am. Fish. Soc. 90:13-20.

Cloudsley-Thompson, J. L. 1961. Rhythmic Activity in Animal Physiology and Behaviour. Academic Press, N. Y.

Cooper, E. L. 1953. Periodicity of growth and change of condition of brook trout (Salvelinus fontinalis) in three Michigan trout streams. Copeia 1953(2):107-114.

Cooper, J. C., and T. T. Polgar. 1981. Recognition of year-class dominance in striped bass management. Trans. Am. Fish. Soc. 110:180-187.

Coutant, C. C., K. L. Zachman, D. K. Cox, and B. L. Pearman. 1984. Temperature selection by juvenile striped bass in laboratory and field. Trans. Am. Fish. Soc. 113:666-671.

Cox, D. K., and C. C. Coutant. 1981. Growth dynamics of juvenile striped bass as functions of temperature and ration. Trans. Am. Fish. Soc. 110:226-238.

Crecco, V. A., and T. F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, Alosa sapidissima, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42:1640-1648.

Crecco, V. A., T. F. Savoy, and L. Gunn. 1983. Daily mortality rates of larval American shad (Alosa sapidissima) in the Connecticut River with changes in year-class. Can. J. Fish. Aquat. Sci. 40:1719-1728.

Cushing, D. H., and J. G. Harris. 1973. Stock and recruitment and the problem of density dependence. Rapp. P.-v. Reun. Cons. int. Explor. Mer 164:142-155.

Deegan, L. A., and B. A. Thompson. 1987. Growth rate and life history events of young-of-the-year Gulf menhaden as determined from otoliths. Trans. Am. Fish. Soc. 116:663-667.

Degens, E. T., W. G. Deuser, and R. L. Haedrich. 1969. Molecular structure and composition of fish otoliths. Mar. Biol. 2:105-113.

Dey, W. P. 1981. Mortality and growth of young-of-the-year striped bass in the Hudson River Estuary. Trans. Am. Fish. Soc. 110:151-157.

Dovel, W. L. 1971. Fish eggs and larvae of the upper Chesapeake Bay. Natural Resource Institute Special Report No. 4, University of Maryland. 71pp.

Eldridge, M. B., D. J. King, D. Eng, and M. J. Bowers. 1977. Role of the oil globule in survival and growth of striped bass larvae. Proc. Annual Conf. West. Assoc. Game Fish Comm. 57:303-313.

Essig, R. J., and C. F. Cole. 1986. Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. 115:34-40.

Fay, C. W., R. J. Neves, and G. B. Pardue. 1983. Species profiles: Life history and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic) - striped bass. U. S. Fish Wildl. Serv. FWS/OBS-82/11.8, TR EL-82-4. 36pp.

Florence, B. M. 1980. Harvest of the north-eastern coastal striped bass stocks produced in the Chesapeake Bay. Pages 29-44. In Clepper (ed.). Proceedings of the Fifth Annual Marine Recreational Fisheries Symposium. Sport Fishing Institute, Washington, D.C.

Francis, R. I. 1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36:883-902.

Fritz, E. S., L. B. Crowder, and R. C. Francis. 1990. Plan for recruitment fisheries oceanography research. Fisheries 15(1):25-31.

Geffen, A. J. 1986. The growth of herring larvae, Clupea harengus L., in the Clyde: and assessment of the suitability of otolith ageing methods. J. Fish Biol. 28:279-288.

Geffen, A. J. 1982. Otolith ring deposition in relation to growth rate in herring (Clupea harengus) and turbot (Scophthalmus maximus) larvae. Mar. Biol. 71:317-326.

Gjosaeter, J., et al. 1984. Ageing tropical fish by growth rings in the otoliths. FAO Fisheries Circular Number 776. 54pp.

Goodyear, P. C. 1984. Analysis of potential yield per recruit for striped bass produced in Chesapeake Bay. N. Am. J. Fish. Manage. 4:488-496.

Gutierrez, E., and B. Morales-Nin. 1986. Time series analysis of daily growth in Dicentrarchus labrax otoliths. J. Exp. Biol. Ecol. 103:163-179.

Haake, P. W., C. A. Wilson, and J. M. Dean. 1982. A technique for the examination of otoliths by SEM with application to larval fishes. Pages 12-15. In C. F. Bryan, J. V. Conner, and F. M. Truesdale (ed.). Proceedings of the Fifth Annual Larval Fish Conference. Louisiana State University Press, Baton Rouge, LA.

Hettler, W. F. 1984. Marking otoliths by immersion of marine fish larvae in tetracycline. Trans. Am. Fish. Soc. 113:370-373.

Hinde, R. A. 1970. Animal behavior: synthesis of ethology and comparative psychology. McGraw-Hill Book Company, N.Y.

Houde, E. D., and L. Lubbers III. 1986. Survival and growth of striped bass, Morone saxatilis, and Morone hybrid larvae: laboratory and pond enclosure experiments. U. S. Fish Wildl. Serv. Fish. Bull. 84(4):905-914.

Houde, E. D., et al. 1990. Egg production and larval dynamics of striped bass and white perch in the Potomac River and Upper Chesapeake Bay. Report to Maryland Department of Natural Resources, Tidewater Administration (Vol I). Chesapeake Biological Laboratory. Ref. No. [UMCEES]-CBL 90-114. 276pp.

Irie, T. 1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3:203-229.

Jones, C. 1986. Determining age of larval fish with the otolith increment technique. U. S. Fish Wildl. Serv. Fish. Bull. 84:91-103.

Jones, C., and E. B. Brothers. 1987. Validation of the otolith increment aging technique for striped bass, Morone saxatilis, larvae reared under suboptimal feeding conditions. U. S. Fish Wildl. Serv. Fish. Bull. 85(2):171-178.

Karakiri, M., R. Berghahn, and H. von Westernhagen. 1989. Growth differences in 0-group plaice Pleuronectes platessa as revealed by otolith microstructure analysis. Mar. Ecol. Prog. Series 55:15-22.

Kellogg, R. L., and J. J. Gift. 1983. Relationship between optimum temperature for growth and preferred temperatures for the young of four fish species. Trans. Am. Fish. Soc. 112:424-430.

Kernehan, R. J., M. R. Headrick, and R. E. Smith. 1981. Early life history of striped bass in the Chesapeake and Delaware Canal and vicinity. Trans. Am. Fish. Soc. 110:137-150.

Koo, T. S. Y. 1970. The striped bass fishery in the Atlantic states. Chesapeake Sci. 11:73-93.

Koo, T. S. Y., and D. E. Ritchie. 1973. Growth of juvenile striped bass, Morone saxatilis, as determined by tagging and recapture. Pages 124-125 (Abstract only). In A. L. Pacheo (ed.). Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic Coast estuaries. Nat. Mar. Fish. Serv. Tech. Publ. No. 1, Mid-Atlantic Coastal Fisheries Center, Highlands, NJ. 338 pp.

Kramer, R. H., and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, Micropterus salmoides (Lacipede), and some related ecological factors. Trans. Am. Fish. Soc. 89:222-233.

Laurs, R. M., R. Nishimoto, and J. A. Wetherall. 1985. Frequency of increment formation on sagittae of North Pacific albacore (Thunnus alalunga). Can. J. Fish. Aquat. Sci. 42:1552-1555.

LeCren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in perch (Perca fluviatilis). J. Animal Ecol. 20(2):.201-219.

Liew, P. K. 1974. Age determination of American eels based on the structure of their otoliths. Pages 124-136. In T. B. Bagenal (ed.) Ageing of Fish. Unwin Brothers Limited, Old Working, Surrey, England.

Lough, R. G., M. Pennington, G. R. Bolz, and A. A. Rosenberg. 1982. Age and growth of larval Atlantic herring, Clupea harengus L, in the Gulf of Maine-Georges Bank region based on otolith growth increments. U. S. Fish Wildl. Serv. Fish. Bull. 80:187-199.

Mansueti, R. J. 1961. Age, growth, and movements of the striped bass, Roccus saxatilis, taken in size selective fishing gear in Maryland. Chesapeake Sci. 2(1-2):9-36.

Mansueti, R. J. 1958. Eggs, larvae, and young of the striped bass, Roccus saxatilis. Ches. Biol. Lab. No. 112.

Markle, C. F., and G. C. Grant. 1970. The summer food habits of young of the year striped bass in three Virginia rivers. Chesapeake Sci. 11:50-54.

Marshall, S., and S. S. Parker. 1982. Pattern identification in the microstructure of sockeye salmon (Oncorynchus nerka) otoliths. Can. J. Fish. Aquat. Sci. 39:542-547.

Merriman, D. 1941. Studies on the striped bass (Roccus saxatilis) of the Atlantic Coast. U. S. Fish. Wildl. Serv. Fish. Bull. 35:1-77.

Methot, R. D., Jr. 1983. Seasonal variation in survival of larval Northern anchovy, Engraulis mordax, estimated from the age distribution of juveniles. U. S. Fish Wildl. Serv. Fish. Bull. 81:741-750.

Miller, S. J., and T. Storck. 1984. Temporal spawning distribution of largemouth bass and young-of-year growth, determined from daily otolith rings. Trans. Am. Fish. Soc. 113:571-578.

Mosegaard, H., H. Svedang, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (Salvelinus alpinus) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45(9):1514-1524.

Mugiya, Y. 1987. Effects of photoperiod on the formation of otolith increments in the embryonic and larval rainbow trout. Nippon Suisan Gakkaishi 53(11):1979-1984.

Mugiya, Y. 1987. Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout. U. S. Fish Wildl. Serv. Fish. Bull. 85(3):395-401.

Mugiya, Y. 1984. Diurnal rhythm in otolith formation in the rainbow trout, Salmo gairdner: seasonal reversal of the rhythm in relation to plasma calcium concentrations. Comp. Biochem. Physiol. 78A(2):289-293.

Mugiya, Y. 1974. Calcium-45 behaviour at the level of the otolithic organs of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 40:457-463.

Mugiya, Y., N. Watabe, J. Yamada, J. M. Dean, D. G. Dunkelberger, and M. Shimizu. 1981. Diurnal rhythm in otolith formation in the goldfish, Carassius auratus. Comp. Biochem. Physiol. 68A:659-662.

Neilson, J. D., and G. H. Geen. 1985. Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile chinook salmon (Oncorynchus tshawytscha). U. S. Fish Wildl. Serv. Fish. Bull. 82:91-101.

Neilson, J. D. and G. H. Geen. 1982. Otoliths of chinook salmon (Oncorynchus tshawytscha): daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci. 39:1340-1347.

Neilson, J. D., G. H. Geen, and D. Bottom. 1985. Estuarine growth of juvenile chinook salmon (Oncorynchus tshawytscha) as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42:899-908.

Olney, J. E., G. C. Grant, and G. Hill. 1985. Relative contribution of three Virginia rivers to spawning activity of striped bass, Morone saxatilis. Nat. Ocean. Atm. Admin., Nat. Mar. Fish. Serv. Compl. Rep. P. L. 89-304. 53 pp.

Otwell, W. S., and J. V. Merriner. 1975. Survival and growth of juvenile striped bass, Morone saxatilis, in a factorial experiment with temperature, salinity, and age. Trans. Am. Fish. Soc. 3:560-566.

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173:1124-1126.

Penney, R. W., and G. T. Evans. 1985. Growth histories of larval redfish on an offshore Atlantic fishing bank determined by otolith increment analysis. Can. J. Fish. Aquat. Sci. 42(9):1452-1464.

Polgar, T. T. 1977. Striped bass ichthyoplankton abundance, mortality, and production estimation for the Potomac River population. Pages 110-126. *In* W. Van Winkle (ed.). Proceedings of the conference on assessing the effects of powerplant-induced mortality on fish populations. Pergamon Press, NY.

Radtke, R. L. 1978. Aberrant sagittae from larval striped bass, *Morone saxatilis*. Copeia 1978(4):712-713.

Radtke, R. L., and J. M. Dean. 1982. Increment formation in the otoliths of embryos, larvae, and juveniles of the mummichog, *Fundulus heteroclitus*. U. S. Fish Wildl. Serv. Fish. Bull. 80:201-216.

Raney, E. C. 1952. The life history of the striped bass. Bing. Ocean. Coll., Yale Univ. Bull. 14:5-97.

Rannou, M., and C. Thiriot-Quievreux. 1975. Structure des otolithes d'un Macroouridae bathyal. Etude au microscope electronique a bayalage. Ann. Inst. Oceanogr. 51:195-201.

Rathjen, W. F., and L. C. Miller. 1957. Aspects of the early life history of the striped bass (*Roccus saxatilis*) in the Hudson River. N. Y. Fish and Game J. 4(1):43-60.

Re, P., and H. C. Rosa. 1986. Daily microgrowth increments in the sagittae of *Dicentrarchus labrax* larvae under controlled conditions. Inv. Pesq. 50(3):397-402.

Redpath, G. S. 1972. Temperature and its effects on the growth and production of juvenile striped bass (*Morone saxatilis*). M. S. Thesis, University of California, Davis. 37 pp.

Reznick, C., E. Lindbeck, and H. Bryga. 1989. Slower growth results in larger otoliths: an experimental test with guppies. Can. J. Fish. Aquat. Sci. 46:108-112.

Rice, J. A. 1987. Reliability of age and growth rate estimates derived from otolith analysis. Pages 167-176. *In* R. C. Summerfelt and F. E. Hall (ed.). Age and Growth of Fish. Iowa State University Press, Ames, Iowa.

Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116:703-718.

Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479-541.

Ritchie, D. E., and T. S. Y. Koo. 1968. Movement of juvenile striped bass in the estuary as determined by tagging and recapture. Ches. Biol. Lab. Rep. No. 68-31. 1pp.

Rogers, B. A., and D. T. Westin. 1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. Trans. Am. Fish. Soc. 110:100-110.

Rogers, B. A., D. T. Westin, and S. B. Saila. 1977. Life stage duration in Hudson River striped bass. University of Rhode Island Mar. Tech. Rep. No. 31. 111pp.

Rosa, H. C., and P. Re. 1986. Diel rhythms in Dicentrarchus labrax (L., 1758) larvae under controlled conditions: swim bladder inflation, feeding, and otolith growth. Inv. Pesq. 49(3):411-418.

Rosa, H. C., and P. Re. 1985. Influence of exogenous factors on the formation of daily microgrowth increments in otoliths of Tilapia mariae juveniles. Cybium 9(4):341-357.

Rosenberg, A. A., and A. S. Haugen. 1982. Individual growth and size-selective mortality of larval turbot (Scophthalmus maximus) reared in enclosures. Mar. Biol. 72:73-77.

Savoy, T. F., and V. A. Crecco. 1987. Daily increments on the otoliths of larval American shad and their potential use in population dynamic studies. Pages 413-431. In R. C. Summerfelt (ed.) Age and Growth of Fish. Iowa State University Press, Ames, Iowa.

Schwassman, H. O. 1971. Biological Rhythms in Fish Physiology VI. Hoar and Randall, ed.

Secor, D. H., and J. M. Dean. 1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, Morone saxatilis. Can. J. Fish. Aquat. Sci. 46:113-121.

Secor, D. H., J. M. Dean, and R. B. Baldevarona. 1989. Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. Rapp. P.-v. Reun. Cons. int. Explor. Mer 191:431-438.

Struhsaker, P., and J. H. Uchiyama. 1976. Age and growth of the nehu, Stolephorus purpureus (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. U. S. Fish Wildl. Serv. Fish. Bull. 74(1):9-19.

Suthers, I. M., K. T. Frank, and S. E. Campana. 1989. Spatial comparison of recent growth in postlarval Atlantic cod (Gadus morhua) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46(Suppl. 1):113-124.

Tanaka, K., Y. Mugiya, and J. Yamada. 1981. Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile Tilapia nilotica. U. S. Fish Wildl. Serv. Fish. Bull. 79:459-466.

Taubert, B. D., and D. W. Coble. 1977. Daily rings in three species of Lepomis and Tilapia mossambica. J. Fish. Res. Board Can. 34:332-340.

Texas Instruments, Inc. 1975. Hudson River ecological study in the area of Indian Point. 1974 Annual Report to Consolidated Edison Co., New York.

Tiller, R. E. 1950. A five-year study of the striped bass fishery of Maryland, based on analysis of the scales. Ches. Biol. Lab. Publ. 85:1-30.

Townsend, D. W., and J. J. Graham. 1981. Growth and age structure of larval Atlantic herring, Clupea harengus, in the Sheepscot River Estuary, Maine, as determined by daily growth increments in otoliths. U. S. Fish Wildl. Serv. Fish. Bull. 79(1):123-130.

Townsend, D. W., and R. F. Shaw. 1982. Daily growth increments in otoliths of blue whiting from above the Arctic Circle. Sarsia 67:143-147.

Trent, W. L. 1962. Growth and abundance of young-of-the-year striped bass, Roccus saxatilis (Walbaum), in Albemarle Sound, North Carolina. M. S. Thesis, North Carolina State College, Raleigh, NC. 66pp.

Tresselt, E. F. 1950. Spawning grounds of the striped bass or rock, Roccus saxatilis (Walbaum), in Virginia. M. S. Thesis, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. 29pp.

Tsukamoto, K., and T. Kajihara. 1987. Age determination of ayu with otolith. Nippon Suisan Gakkaishi 53(11):1985-1997.

Ulanowicz, R. E., and T. T. Polgar. 1980. Influences of anadromous spawning behavior and optimal environmental conditions upon striped bass year class success. Can. J. Fish. Aquat. Sci. 37:143-154.

Uphoff, J. H., Jr. 1989. Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. Trans. Am. Fish. Soc. 118:251-263.

Van Winkle, W., and K. D. Kumar. 1982. Relative stock composition of the Atlantic Coast striped bass population: Further analysis. NUREG/CR-2563; ORNL/TM-8217. Oak Ridge National Laboratory, Oak Ridge, TN. 38pp.

Van Winkle, W., B. L. Kirk, and B. W. Rust. 1979. Periodicities in Atlantic coast striped bass (Morone saxatilis) commercial fisheries data. J. Fish. Res. Board Can. 36:54-62.

Victor, B. C. 1982. Daily otolith increments and recruitment in two coral-reef wrasses. Mar. Biol. 71:203-208.

Volk, B. C., R. C. Wissimar, C. A. Simenstad, and D. M. Eggers. 1984. Relationship between otolith microstructure and the growth rate of juvenile chum salmon (Oncorynchus keta) under different prey rations. Can. J. Fish. Aquat. Sci. 41:126-133.

Ware, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503-2512.

Warlen, S. M. 1988. Age and growth of larval Gulf menhaden, Brevoortia patronus, in the Northern Gulf of Mexico. U. S. Fish Wildl. Serv. Fish. Bull. 86(1):77-90.

Warlen, S. M., and A. J. Chester. 1985. Age, growth, and distribution of larval spot, Leiostomus xanthurus, off North Carolina. U. S. Fish Wildl. Serv. Fish. Bull. 83(4):587-599.

Weber, D., and G. J. Ridgeway. 1967. Marking Pacific salmon with tetracycline antibiotics. J. Fish. Res. Board Can. 24(4):849-865.

Wild, A., and T. J. Foreman. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Int. Am. Trop. Tuna Comm. 17: 507-557.

Wilson, K. H., and P. A. Larkin. 1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon. Can. J. Fish. Aquat. Sci. 39(10):1335-1339.

Zweifel, J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes - a general model. U. S. Fish Wildl. Serv. Fish. Bull. 74:609-621.

VITA

LISA L. KLINE

Born in Pottstown, Pennsylvania, 19 October 1961. Graduated from Emmaus High School, Emmaus, Pennsylvania in 1979. Earned B.S. in Marine Biology from Millersville University of Pennsylvania, Lancaster, Pennsylvania in 1983. Entered masters program of the School of Marine Science, College of William and Mary in 1985. Bypassed masters and entered doctoral program in 1987. Employed by the Maryland Department of Natural Resources, Annapolis, Maryland, in July 1990.