Spring 1988

Age and Growth of the Tautog, *Tautoga onitis* (Pisces: Labridae), from Lower Chesapeake Bay and Coastal Waters of Virginia

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AGE AND GROWTH OF THE TAUTOG, *TAUTOGA ONITIS* (PISCES: LABRIDAE), FROM LOWER CHESAPEAKE BAY AND COASTAL WATERS OF VIRGINIA

by

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B. S. June 1979, Virginia Polytechnic Institute
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A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

Old Dominion University
May 1988

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ABSTRACT

AGE AND GROWTH OF THE TAUTOG, TAUTOGA ONITIS (PISCES: LABRIDAE), FROM LOWER CHESAPEAKE BAY AND COASTAL WATERS OF VIRGINIA

The tautog, *Tautoga onitis* (Pisces: Labridae), is rapidly gaining popularity in Virginia by anglers, spearfishermen and specialized commercial interests. In Virginia, tautog are seasonally abundant on hard bottom substrates in nearshore (ca. 2-10 m) habitats and inhabit offshore wrecks and reef areas (ca. 10-30 m) year round. Habitat restriction and slow growth of the species coupled with recent technological advances in marine electronics which simplify locating tautog populations by user groups may contribute to overexploitation of tautog within the region.

Tautog were collected over a two year period from the lower Chesapeake Bay and nearshore waters of the Atlantic Ocean to determine age and growth of the species within the region. Fish were initially aged using three structures; otoliths, opercle bones, and scales. Validation results indicate that tautog can be aged successfully with opercle bones. Annulus formation occurs during the protracted spawning season (May-July) in all age groups. Maturation occurs as early as age three in both sexes. Additionally, the observation of two adult male phases is noted.

Tautog are long-lived (25 yrs or more) and attain relatively large sizes (ca. 800 mm TL) slowly (k-values of 0.09 - 0.12). Growth rates were calculated by two methods; back-calculations and the Von Bertalanffy equation. The analysis of growth rates between the sexes were similar; however, males attain greater total asymptotic length but do not necessarily attain greater ages than females. A comparison of growth parameters made with studies from northern areas indicate that tautog attain greater size at an earlier age in Virginia waters. Comparisons of growth parameters are made with labrids and other reef-dwelling fishes. Management recommendations are based on habitat preference, growth rate and sexual strategy.

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ACKNOWLEDGMENTS

There have been many people who have assisted me in this project over the years and some may not be mentioned but will surely not be forgotten. Dr. Ray Birdsong (ODU) and Dr. Thomas Munroe (VIMS) provided the impetus for my research and developed my knowledge of marine biology. Dr. Munroe also provided invaluable unpublished data. Dr. Joseph Loesch (VIMS) and David Hata helped with fisheries statistics. Dirk Peterson aided me in the initial data processing and the rest of the grad students gave me room to work. People who aided in the collection of specimens include Michael Bucy, John Witcher (who almost lost a boat in the process), Mark, Art and Kenneth Hodges, George and William Susewind, Bert Parolari, Lewis Gillingham, James White, Dr. David Wright, and especially Melvin (hotshot) Harrel. Dr. Birdsong, Dr. Munroe, Dr. Daniel Dauer, and Dr. Robert Rose helped with editing this manuscript. I have no thanks for my labrador, Shilo, who ate several specimens, but I have the utmost respect and love for my wife who endured my "tog bones" and encouraged me during this study.

This thesis is dedicated to my daughter,

Sarah Anne,

born 19 February 1987.

Plate 1. Female tautog, *Tautoga onitis* (Pisces: Labridae), 434 mm total length.

INTRODUCTION

The tautog, *Tautoga onitis*, (Plate 1) is a member of the family Labridae and, along with the cunner *Tautogolabrus adspersus*, are the northernmost members of this family in the Western North Atlantic. Tautog range from Nova Scotia to South Carolina (Hildebrand and Schroeder, 1928; Robins et al., 1986). In Virginia, specimens have been taken along the seaside Coast as far as 65 km offshore. Within the Chesapeake Bay tautog occur from Gwynn's Island near the mouth of the Rappahannock River to Sandy Point on the Eastern Shore (Hildebrand and Schroeder, 1928). They are common around jetties and riprap islands in water less than 2 m and as deep as 75 m on submerged offshore wrecks.

The possibility of overfishing this species is increasing as the tautog gains in popularity with anglers and spearfisherman in Virginia (Bain, 1984; Arrington, 1985). The number of Virginia Salt Water Fishing Tournament citations for catches exceeding 9 lbs has climbed from an average of 122/yr for the period 1976-1980 to an average of 282/yr for the years 1981-1986. Commercial statistics from 1922 (Hildebrand and Schroeder, 1928) to present (Virginia Marine Resources Commission, VMRC) show little change in weight of reported catch of the species. However, officials within the VMRC (Gillingham, pers. comm.) believe that these landing estimates (roughly 2000 lbs/yr) are insignificant compared to the unreported catch by rod-and-reel commercial and recreational fishermen.

The biology and growth rate of the species may also render tautog stocks in Virginia especially susceptible to overexploitation. Suitable hard-bottom habitat is limited and discontinuous in Virginia. Submerged wrecks, artificial reefs, jetties and the artificial islands of the Chesapeake Bay Bridge Tunnel are primary areas of tautog concentrations and fishing pressure on these isolated areas can be intense. Cooper (1967) found tautog in Rhode Island to be slow-growing with males requiring 10 years and females 9 years to reach an eviscerated weight of 900 g. The oldest female fish aged by Cooper (1965) was 22 years and the oldest male 27 yrs. A fish of 34 years is noted, but not included in the study. Various studies (Cooper, 1965; Briggs, 1977; Turner et al., 1983; Matheson and Huntsman, 1984; Moore and Labisky, 1984; Manooch and Mason, 1984; and Harris and Grossman, 1985) have indicated that slow-growing species concentrated in reef areas can be greatly depleted by fishing pressure. Recent technological advances in LORAN and recording depth finders and their present general availability to fishermen have simplified locating even small populations of tautog. Pressure on tautog populations can at times be intense and my experience gained as a researcher, sportfisherman, diver and mate on charter vessels over twelve years in Virginia waters indicates that many of the more popular fishing areas are being detrimentally affected. Accurate age/growth data are critical in the assessment of population fluctuations and the effects that predation and fishing pressure have on tautog populations in Virginia.

Cooper (1966), Olla et al., (1974) and Briggs (1977) noted an inshore-offshore spawning migration in northern populations of tautog, but no significant north-south component to this migration was recognized. Additionally, as one moves southward in the mid-Atlantic Bight, variation in temperature, habitat availability, food and other ecological factors indicates the necessity of regional studies of growth differences between populations. Tautog occurring in Virginia waters may thus comprise a separate population with growth characteristics different from those reported for populations in more northern waters.

The objectives of this study were to:

(1) examine age and growth in the tautog from Virginia;

(2) to determine the time and periodicity of spawning; and

(3) compare these data with those from previous published studies from more northern areas.

MATERIALS AND METHODS

Fish Collection

Tautog frequent rocky substrates and wrecks and are generally unavailable to collecting methods such as gill nets or trawls. The fish used in this study were sampled by rod and reel and spearfishing on offshore wrecks and the Chesapeake Bay Bridge Tunnel. Collection of fish representing the complete size range for the species was attempted. Few young fish less than 200 mm total length (TL) were seen. Since juvenile tautog occur primarily in inshore grass beds in the Chesapeake Bay region (Hildebrand and Schroeder, 1928), their absence on the reefs and wrecks which were sampled was not unexpected.

Samples were taken from nine locations within the Chesapeake Bay and offshore (Figure 1). The area bounded by the locations encompassed 3900 km^2, thus ensuring representation of a wide variety of ecological conditions characteristic of tautog habitat in Virginia. Station depths varied from 2 to 35 m (Table 1). Substrate types, abundance of fish species and encrusting organisms associated with each station were variable. From March 1984 to July 1986, 173 tautog were collected. Approximately 65% of fish sampled were taken from locations 3, 4 and 5 with small samples taken from most locations; therefore, data from all stations were combined in the analysis.

<u>Data Collection from Field Samples</u>

For each fish, information on location and date of capture, sex, standard length (SL), total length (TL), total weight (WT), and weight of gonads was recorded. Total and standard length measurements were made with a meter stick affixed to a fishboard. Measurements were recorded to the nearest 5 mm. Gonads were weighed to the nearest 5 g on a triple beam balance. Total weight was determined on a fan dial scale to a precision of 5 g. After removal, ovaries were longitudinally sectioned and placed in Gilson's solution (Simpson, 1951) for further study.

Sex was initially determined by pigmentation, dimorphism in mandible shape, and slope of the forehead. Males usually exhibited a blunt forehead with a more massive mandible, while in females the mandible and forehead profile is more tapered. Larger males typically exhibit white markings on the caudal, ventral and dorsal fins, and chin that are visible under water. Overall pigmentation of larger males is gray, whereas females and smaller males tend to be a mottled brown. Final determination of sex was through gonad examination. This was necessitated by the apparent lack of any external sexual dimorphism in about 15% of all male fish examined.

Structures for Age and Growth Studies

In order to assess age from scales or bony parts in temperate fishes a detectable pattern with which a time scale can be associated must be present. In addition, this mark or pattern must be repeated annually (Bagenal and Tesch, 1978). In this study, scales, otoliths and opercles were selected and removed for aging purposes.

A scale sample from the first 21 fish was removed from the region immediately above the lateral line between the pectoral fin base and the dorsal fin base. Scales were then labeled, dried and stored in scale envelopes for later examination under 25X magnification.

Saccular otoliths were removed after sagittaly sectioning the cranium with a bone saw. Each sacculus and exposed sagitta was removed with forceps. The 2-4 mm otolith was then separated from the sacculus by rubbing between the palm and forefinger. Otoliths were stored in glycerine or isopropyl alcohol. Placement of otoliths in alcohol tended to "clear" them of discernible annuli and is not recommended. The otoliths were examined in an oil immersion under reflected and transmitted light at 25X and 50X magnification. The number of annuli in each otolith was recorded and later compared to opercle age determinations.

Each opercle bone was removed with a scalpel by disarticulation at its apex. The bones were boiled for two to three minutes to remove adhering soft tissue, brushed clean under running tap water, and then allowed to dry for 48 hours. After drying, annuli were counted for both right and left opercles using transmitted light. For each opercle four readings were made at 1X and two at 6X magnification. All annuli that were continuous within the contours of the opercle were counted. Brander (1974) and Ricker (1969) recommended that consistency in otolith, or in this case opercle, readings requires that all age determinations be made by the same person. Thusly, bias will not significantly affect either survivorship curves or estimations of growth since the probability of age misallocation will be similar for all age classes.

The opercular radius (OR), defined as the distance from the apex center to the midpoint of posterior margin, was measured with dial calipers to a precision of 0.1 mm (Figure 2). Similarly, measurements (to 0.1 mm) were made along this axis to each annulus to determine annual growth. After recording and measuring annuli, opercles were labeled with indelible ink and stored in envelopes. Deformed opercles, or those which had been altered by spear point wounds, were not used in the analyses.

Compaction of daily growth rings on the opercle during the time of gonadal tissue accumulation and subsequent spawning produces an opaque zone which contrasts against a wider hyaline band of rapid growth. In annuli older than the second annulus the opaque zone tended to form a somewhat wider band instead of a sharp line suggesting a protracted period of slow growth. Following the terminology of Pannela (1974), an annulus was defined as the sharp transition from a hyaline to an opaque zone on the opercle. Only annuli that were discernible and continuous from ventral to dorsal margin of the bone were considered true annuli. Other horizontal marks that did not meet these criteria were not included in the annuli count. Yearly growth on the opercles was interpreted as being equal to one hyaline zone plus one opaque zone.

Initially, annuli of both opercles from each fish were counted. Differences in age estimation between left and right opercles from the same fish occurred in less than 10% of comparisons. When differences between left and right opercles were noted, age was determined from the opercle in which annuli were the most clearly defined.

A standard least squares Type I linear regression (Sokal and Rohlf, 1981) was adapted for use in LOTUS [R] spreadsheet format (Jeanty, 1984) to describe relationships between total length, standard length, opercle radius, total weight and age. Determination of time at annulus formation was adopted from Nose et al.,(1955) and Cooper (1965). Mean length at age was computed from back-calculations (following Bagenal and Tesch, 1978) by substituting mean distance from apex center to each annulus (R) into the regression equation, TL = a + b(R), where a = y intercept and b = slope. Covariance analysis (ANCOVA) in

SPSS-X was used to compare age at length between the sexes. The Von Bertalanffy growth equation was used, following Gulland (1976), to compute length at age.

RESULTS AND DISCUSSION

Morphometrics

Comparison of Growth Between Sexes

A total of 173 tautog ranging in size from 240 to 765 mm were collected. 167 of these fish were usable for age and growth study, 98 were males and 69 were females. The opercles from the 6 remaining fish were damaged and not used in age analysis.

Male fish ranged from 265 mm to 765 mm TL and weighed from 335 to 6895 g. Ages for male tautog ranged from 2 to 18 years. Female fish ranged from 240 mm to 750 mm TL and weighed from 240 to 7390 g. Ages for females ranged from 2 to 21 years.

Results of ANCOVA analysis indicated no significant difference between slopes of the regression equations of length at age for male and female tautog ($F = 1.337$, $P < 0.25$). Additionally, the analysis of covariance is nonsignificant for homogeneity of the means around the regression slope ($F = 2.107$, $P < 0.15$). There were no statistically significant difference in the equations of age on length between male and female tautog in this study. These results contrast the findings of Cooper (1965) for northern tautog populations.

Although no statistical differences were found between male and female tautog at length at age from Virginia, in all further analysis data were maintained separately. Justification for this include consideration of Cooper's (1965) results from a larger sample and, more importantly, the complexity of reproductive strategies within the family Labridae (Robertson and Warner, 1978; Dipper and Pullin, 1979). This separation by sex also facilitated the ability to compare results between northern and southern study areas.

Standard Length to Total Length Relation

Both total and standard length measurements were recorded because of the possibility of allometric growth of the caudal fin. Data from both sexes were combined to generate a regression equation and correlation coefficient for SL on TL (TL = 18.735 + 1.158 SL). The high correlation (n = 173; r^2 = 0.96) between SL and TL prompted the use of TL as the more easily and reliably obtained measurement.

Length to Weight Relation

Length to weight relationships were calculated separately for males and females using data from all collected specimens (Figures 3 and 4). Data were logtransformed to more closely approach linearity in the following regression equations:

males ($n = 103$; $r^2 = 0.97$):

$$WT = -3293.7 + 12.0\ TL$$

$$\log WT = -4.32 + 2.86 \log TL$$

females ($n = 70$; $r^2 = 0.98$):

$$WT = -3469.2 + 12.6\ TL$$

$$\log WT = -4.57 + 2.95 \log TL$$

combined ($n = 173$; $r^2 = 0.98$):

$$WT = -3336.4 + 12.6\ TL$$

$$\log WT = -4.47 + 2.92 \log TL$$

where WT = weight (g), TL = total length (mm). Derived length at age estimates from the von Bertalanffy growth equations were later used in these regression equations to calculate weight at age.

Although correlation coefficients were high in the analysis of weight on total length, considerable variation in weight within age groups was observed. This variation in weight at length can be attributed to geographic population location and associated environmental conditions, seasonality (date and time of capture), sex, maturity, stomach fullness and age. Le Cren (1951), Bagenal and Tesch (1978) and others have observed that stages in the ontogenetic development of fish contribute to changes in the relationship of weight on length. These growth stanzas thus contribute to regression variation of WT on TL. Length to weight relationships derived from a regression equation must be considered only gross estimates of weight at age. Better estimates could be attained through sample partitioning by factors which contribute to this variation; however, such an extensive sampling regime was beyond the scope of this study.

Age Estimations

Annulus validation

Ring compaction at the outer edge of scales in these long-lived fish made distinguishing annuli or even scale edge difficult (see Cooper, 1965). Further, scale abrasion and surface area damage were common and greatly hindered age estimates. In fish with less than four annuli there was good agreement between opercle annuli and scale annuli; however, accurately aging older fish by scales was not possible and led to the abandonment of this method.

Comparisons of otoliths and opercle bones from 27 fish indicated close agreement in readings of annuli from each structure, especially in younger fish (Table 2). Otoliths exhibited a thickening of the nucleus core that made it difficult to discern any microstructure in this region. Sanding of the otoliths on 2600 grit jeweler's paper (see Pannela, 1974) proved difficult and in most cases also blurred or removed annuli on the outer edge of the otolith. The high correlation of annuli number from opercle bones and otoliths and the greater ease of extraction and reading of opercula led to their exclusive use in aging tautog in this study.

Opercle Structure

Opercle structure in the tautog has been described by Cooper (1965). Roughly triangular in shape, with a pronounced notch in the ventral margin, the opercle bone tapers in thickness from the articular fossa to a fine edge on both the posterior and ventral margins. The dorsal margin is a thicker band of opaque bone with parallel striations which run perpendicular to the annuli. The lateral surface of the bone is convex. The articular apical center, as defined by LeCren (1947), McConnell (1952) Bardach (1955), and Cooper (1965), is the center of the high ridge projecting from the medial surface of the opercle (Figure 2).

In using opercula for aging purposes, a regression must exist between some measure of this bone and fish length. In this study a linear relationship existed between the opercle radius and total length (Figure 5). The regression equation describing this relationship is:

$$TL = -2.410 + 0.0870\ OR$$

$$\log TL = 1.292 + 0.8687 \log OR$$

$$(n = 167;\ r^2 = 0.94)$$

A log transformation of the data ensured linearity of regression by the least squares method (Sokal and Rohlf, 1981) and eliminated any heteroscedasticity (or difference in variance).

Cooper's (1965) tag and recapture research on tautog has verified that annuli on opercle bones in tautog do represent year marks and that these marks are indicative of rate of growth throughout the year. Beamish and McFarlane (1983) noted validation problems with age and growth studies and emphasized the need for age verification. Therefore, I duplicated a portion of the validation methodology for Virginia tautog.

Comparison of the initial and final readings of the four 1X observations of opercle annuli (sexes combined) revealed a total of 135 (80%) agreement in readings. Of the remainder, 31 (19%) differed in age by one year, and 1 (1%) by 2 years. The high level of agreement between opercle readings, high linear correlation ($r^2 = 0.94$) between TL and OR, and time of annulus formation were similar to the results of Cooper (1965) and Munroe (unpubl.). Further, tautog opercular annuli satisfy the conditions of Van Oosten (1929), i.e., the opercle radius has a high correlation with total length ($r^2 = 0.94$); the number of annuli increases with size; putative annuli are closely correlated on opercles of all age classes; and back-calculated lengths, compensated for annular growth, closely agreed with observed values for length at age. Removing, preparing and "reading" opercles is also an easier task than for otoliths. The main disadvantage to aging with opercles is discerning early annuli in older fish due to thickening of the opercle buttress zone at the articular apex. These results supported the use of opercle bones instead of scales or otoliths for aging tautog in this study.

Time of Annulus Formation

Plots of last annulus width (A) against date of capture represents seasonal growth of the opercle. Minimal annulus width reflects time of formation. However, a randomized plot results if fish are not of similar age or reflect similar annular incremental growth. Sample sizes of individual age groups were inadequate to determine time of annulus formation. Therefore, annulus width (A) from fish Age 3-4, 6-7 and 9-10 were grouped (Figure 6). (The similarity in incremental annual growth justified combining age groups for this analysis.) Minimal incremental growth and subsequent annuli formation occurred during the months May, June and July. Annuli formation did not occur in any other month. The collection of data from widely separated geographic areas accounts for the variation in time of annulus formation. Cooper (1965) collected data from a geographically smaller inshore area and subsequently determined that annuli formation for Rhode Island tautog occurred in May commensurate with spawning activity.

Estimation of growth

Back-calculation of Total Length

Back-calculations of TL at age were derived for both sexes from logarithmic regression formula of OR against TL where the:

$$\log TL = 1.2772 + 0.8774 \log OR$$

$$\text{males } (n = 98;\ r^2 = 0.94)$$

and,

$$\log TL = 1.2994 + 0.8658 \log OR$$

$$\text{females } (n = 69;\ r^2 = 0.96).$$

Slope and intercept values from these equations were used in the back-calculated length equation of Ricker (1975):

$$\log Ln = \log TL + b(\log Rn - \log Rt)$$

where:

Ln = total length at year n

TL = total length at capture

b = slope of body-bone regression

Rn = opercle radius at year n

Rt = opercle radius at capture

Substitution of slope and intercept values gave the equations:

$$\text{(males)}\ \log Ln = 1.2772 + 0.8774(\log Rn - \log Rt)$$

$$\text{(females)}\ \log Ln = 1.2994 + 0.8658(\log Rn - \log Rt).$$

Calculated lengths by sex were then independently determined through substitution of logarithmic values for average TL and OR by age class. The antilog of this value is the actual calculated total length (Tables 3 and 4).

On review of these tables, a similar pattern in growth between male and female fish is detected. Male fish grew to a TL of 338 mm at Age 5 and 500 mm by Age 10. Females, reached a TL of 355 mm at Age 5 and 514 mm at Age 10. Mean annual increments of growth were also very similar between the sexes, with the exception of calculated growth after Age 14 in which small sample size may have influenced the data. The effect of sample size became especially evident for Age 20 females which had a negative growth increment.

Von Bertalanffy Growth Parameters

Parameters of the von Bertalanffy growth equation were derived from back-calculated length-at-age values. Following Gulland (1976), Walford lines and estimates of K and L_{mx} were derived where:

$$L_t = L_{mx}\ [1 - e^{-k(t-to)}]$$

L_t=length at age t; t = age (years)

L_{mx} = asymptotic maximum length

K = calculated growth coefficient

t_o = theoretical time of zero length.

Resulting parameters and equations calculated for male and female fish are as follows:

(males) K = 0.09442, L_{mx} = 799.71

$t_o = -0.7225$

$$L_t = 799.71[1 - e^{-0.09442(t + 0.7725)}]$$

(females) K = 0.1214, L_{mx} = 704.81

$t_o = -0.68345$

$$L_t = 704.81[1 - e^{-0.1214(t + 0.68345)}].$$

Estimates of empirical length at age compared favorably with both back-calculated estimates and observed growth (Table 5).

K-values for tautog indicated that females grew at a slightly faster rate, whereas L_{mx} values indicated a greater TL for males. A plot of calculated L_t values is shown (Figure 7). Males achieved 50% of L_{mx} by Age 7 and 75% by Age 14. Correspondingly, females reached 50% of L_{mx} by Age 5 and 75% by Age 11. The calculated values indicated a greater size and longevity for males. This is supported by Cooper (1967), who indicated a life span of 27 years for males and 22 years for females, with the oldest fish aged at 34 years. Cooper (1965) theorized that females may reach senescence at an earlier age.

Comparison of incremental growth between the sexes (Figure 8) indicated greatest growth in TL occurred during the first year of life and that the rate decreased in each subsequent year. Females maintained a higher incremental growth until age five. Cooper (1965) concluded that, for both sexes, the largest yearly increase in TL occurred in the second year. Further comparison of these data indicated that tautog in Virginia were twice the TL of those in Rhode Island at formation of first annulus. Incremental growth after the second year through age 10 or 11 were comparable for both geographic areas. After age 10-11, yearly TL increments of Rhode Island fish rapidly decline. Growth in tautog from Virginia apparently does not diminish as rapidly.

Growth equations were developed by Cooper (1965) were:

$$\text{(males) } L_t = 664[1-e^{-0.09108(t + 1.66238)}]$$

$$\text{(females) } L_t = 506[1-e^{-0.15189(t + 0.95220)}].$$

These equations indicated appreciably smaller L_{mx} values for both male and female fish in Rhode Island. K-values from Rhode Island also indicate faster rate of growth in female fish and are comparable to results of the present study.

The comparison of k-values between Rhode Island and Virginia tautog supports the contention that rate of growth (k) for tautog is an intrinsic value and is independent of geographic location. Variation in physical or environmental factors would, however, account for differences in both TL and WT per age between these cohorts.

Reproductive Biology

Sexual Maturation

Gonadal maturation was evident in both sexes by Age 3. Age 2 fish were taken in late March and early April with immature gonads. No Age 2 fish were collected later than April; therefore, subsequent development of gonadal tissue could not be ascertained in this age group. Further, absence of specimens younger than Age 2 precluded an absolute determination of age at maturity. Previous work by Chenoweth (1963) and Cooper (1965), Stolgitis (1970) and Briggs (1977) in Rhode Island, Massachusetts and New York, respectively, indicated that sexual maturity is achieved in males at Age 3 and females at Age 4. However, Olla and Samet (1977) noted the collection of sexually mature tautog "which were of a much smaller size and younger age than has previously been reported." No determination of spawning participation in these small fish was noted.

Gonadal Maturation and Annulus Formation

A gonadosomatic index (GSI) was calculated for all female fish using the formula:

GSI = weight of gonads x 100 / total body weight.

A graph of the computed GSI values against date of capture (Figure 9) indicated peak spawning condition during the months of May, June and July. Ripe fish were collected from offshore sites as late as July and early August. However, the GSI from Chesapeake Bay sites began to decrease in June. These observations as well as those of Munroe (unpublished), are the only evidence of an offshore cohort of tautog in spawning condition.

In northern inshore study areas, Stolgitis (1970) determined that the spawning period of tautog in Massachusetts extended from May to August. In Rhode Island tautog, Chenoweth (1963) also found peak spawning in early June-July. Maximum GSI suggests a similar spawning period in Virginia. This runs counter to studies (Berrien et al., 1978) which suggest an earlier spawning time at lower latitudes for the species. However, the collection of fish in mature reproductive condition from offshore sites in Virginia may have contributed to this variation.

The comparison of annual incremental opercle growth (Figure 6) with collection data on gonad condition and the average gonadosomatic index (GSI) (Figure 9) reveals that annulus formation in Virginia occurs commensurate with gonadal maturation in late spring or during spawning in June and July. The formation of an opercular spawning annulus in this fashion is supported by Cooper's data (1965) for the tautog and by Bardach (1955) in the yellow perch, *Perca flavescens*, among others. Chenoweth (1963) observed a body weight decline during ovarian development. This decline in physiological condition supports annulus formation between time of ovarian development and the following resumption in somatic growth. However, annulus formation in tautog cannot be directly attributed to production of mature gonadal tissue or spawning since annuli are found in sexually immature fish during this same time period. Other physiological or environmental factors apparently interplay in this process. Iles (1974) suggests that inherent physiological rhythms associated with spawning may retard somatic growth in sexually immature fish.

Cooper (1967) determined that annuli in Rhode Island tautog formed in late or middle May, at the start of spawning. Virginia tautog were collected over a wider geographic area and formed annuli over a longer period of time (May - July). There was no indication of the formation of a second annulus during the year. Possible explanations for the extended annulus formation time in Virginia populations of tautog include: (1) a general trend for smaller fish to form annuli at a slightly earlier date than larger fish. This pattern agrees with observations that suggest younger and smaller fish are more active at lower water temperatures (Olla et al., 1974; Olla et al., 1980; Cooper, 1966). (2) Since tautog were not collected at regular intervals, data were analyzed independent of the year in which collections were made. Annual environmental variation contributes to variation in annulus formation time. (3) A more extensive sampling area and collection site diversity may contribute to variation. (4) The probability of serial spawning in tautog exists. Ovary development and egg size differentiation support the laboratory observation by Olla and Samet (1977) of serial spawning. If serial spawning is the normal mode of reproduction, previous work on fecundity estimates (Chenoweth, 1963) for the tautog may be faulty.

Sexual Strategy

Comparison of von Bertalanffy growth coefficients between northern and southern study areas indicated a similar difference in growth rates between male and female tautog. Higher rate of growth and apparent longevity of males may reflect higher energy costs of reproduction for females, or indicate the possibility of sex-inversion (protogynous hermaphroditism), a common mode of reproduction in labrids. Cooper (1965) found that female growth exceeds male growth until Age 4. Similar results were obtained in this study (Table 5), but, male growth did not surpass female growth until age 12. Warner (1975b) and Dipper et al. (1977) found similar changes in growth curves of other labrid species coincident with the time of sexual inversion.

The possibility of tautog protogyny is further supported by the observations of two adult male phases in tautog. External dichromatic color and morphological characteristics were used to distinguish sex for tautog in this study. However, approximately 10-20% of tautog, originally identified as females based on external characteristics, were later determined through dissection to be males. These differentiation problems were generally limited to males under 10 years of age. No females were missclassified as males on the basis of external characteristics. Warner and Robertson (1978) label sex-changed males forms in labrids as diandric. It is not presently known in tautog if the characteristic "white-chin" male form is a result of sex change or development of secondary male characters. Therefore, smaller males which externally resemble females will be referred to as Type II males.

Body pigmentation of Type II males and females is mottled brown, with no distinct pattern (Plate 1). Type I (white-chin) males exhibit color pattern, jaw and forehead morphology characteristic of the largest males. The general body pigmentation is gray with distinctive white markings on the ventral and dorsal margins of pectoral and caudal fins and on the chin. The skull and mandibular structure of Type I males is blunter and more massive than that of Type II.

The presence of two male forms in tautog has not been previously addressed in the literature. Olla and Samet (1977) mention the presence of smaller fish (size and sex not specified) that lacked characteristic mandible dimorphism. They attributed these differences to sequential development of male characteristics. This character development theory cannot be disproved, but, due to a wide overlap in size of Type I and Type II males, it seems unlikely that growth alone controls development of secondary male characters. Diandric forms have been shown to indicate sex-reversal (Warner, 1975a) and are the result of selection through mating behavior (Warner and Robertson, 1978; Roberston and Warner, 1978).

Within labrids both gonochoristic and hermaphroditic modes of reproduction are known with hermaphroditism being more common. Various researchers have noted that protogyny and diandric male forms are prevalent in both tropical and temperate labrids from the Atlantic and Pacific (Robertson and Choat, 1974; Warner, 1975b; Warner and Robertson, 1978; Dipper and Pullin, 1979). Comparison of these reproductive observations with tautog spawning behavior and color patterns suggests that a more complex tautog reproductive system may exist.

Studies of tautog courtship and spawning behavior under laboratory conditions indicate multiple spawning (Olla and Samet, 1977; Olla et al., 1981). Territorial behavior by a dominant male and interference or sneak spawning by smaller male tautog was observed in experiments. These strategies, coupled with presence of male forms, are similar to the reproductive strategies of hermaphroditic scarids (Warner and Downs, 1977; Robertson and Warner, 1978) and other labrids, especially Thalassoma bifasciatum (Warner and Robertson, 1978), Labrus ossifagus (Dipper and Pullin, 1979) and Thalassoma lunare (Robertson and Choat, 1974). Robertson and Choat (1974) postulated that the mimetic trait of Type II males may increase the chance of spawning through interference. Further, Warner (1975a) theorized that protogyny is a likely antecedent in systems characterized by such dichotomous male mating strategies.

A sex ratio skewed to males in older age classes may be an indication of protogyny in many fishes (Sadovy and Shapiro, 1987). A Chi-square analysis of the total sample (X^2 = 5.036, d.f. = 1) indicates a significant difference from a 1:1 ratio. Morever, in a comparison of sex ratio within year classes from a data base consisting of almost 600 tautog, Munroe (unpubl.) found the ratio became increasingly skewed to males at older ages. This can be attributed to either greater longevity of males or sex-inversion of females. An analysis of these data (Table 6) indicated that larger (and older) tautog cohorts are predominantly composed of males. Personal SCUBA observations support this contention. Population structure on isolated offshore shipwrecks is primarily composed of mid-size (300 - 500 mm TL) male and female tautog. Larger (> 500 mm TL) fish compose only a small fraction of the total wreck population and are predominantly Type I males. This pattern, however, did not seem to be as evident on the more extensive rock and concrete piling habitat typical of the Chesapeake Bay Bridge Tunnel.

The ecological conditions characteristic of small isolated wrecks are favorable for resource partitioning and development of territoriality. Such systems favor the likelihood of sex change in hermaphroditic species (Emlen and Oring, 1977; Warner, 1982; Warner and Robertson, 1978). As resources and population size increase, selection pressure for dominant male systems decreases as does the potential for sex change (Emlen and Oring, 1977; Warner and Hoffman, 1980). The plasticity of reproductive behavior in tautog, the presence of two male forms, the preponderance of protogynous hermaphroditism in labrids, and the discontinuous distribution of key resources in the study area all suggest the likelihood of protogynous hermaphroditism in tautog. Although Olla and Samet (1977) consider the possibility of hermaphroditism in tautog to be remote, the existing weight of evidence for this species and comparison with hermaphroditic labrids suggest the need for a detailed histological study of tautog gonadal development.

Daily movements and Seasonal Occurrence

Olla et al., (1974) noted a marked decrease in the activity of tautog in water temperatures less than 10°C. At these temperatures they noted a fall migration of larger and older fish (>25 cm, >4 yrs old) to offshore locations. Spring movement from offshore wintering areas to inshore spawning sites are noted by Chenoweth (1963), Cooper (1966), Stolgitis (1970), Olla et al., (1974), Briggs (1977), and Olla et al., (1979). Seasonal population fluctuations on Virginia study sites do occur. However, the pattern of movement in Virginia may not be as well-defined as the migration pattern in northern study areas. Although data is lacking from offshore sites in previous studies, it is apparent that not all Virginia tautog participate in a spawning migration. This is supported by the collection of tautog in peak spawning condition on both inshore and offshore sites throughout the summer. Additionally, large fish (> 25cm) are encountered on inshore sites during the winter months.

Daily activity, patterns of movement, and migration of tautog in New York have been shown to be size dependent (Olla et al., 1974). Larger fish (>25 cm) had a wider home range and traveled longer distances to feeding areas. Smaller fish remained close to structure. This pattern is repeated in Virginia. Smaller fish, when pursued, were more likely to seek shelter within structure (i.e. wrecks and large rock areas) while larger fish often circled the structure at distance or swam to smaller isolated areas of structure. Further, large tautog were collected on several sites with remains of blue mussel, *Mytilus edulis*, in the digestive tract. Nearest observation of this food species was on buoy chains or stanchions on the Chesapeake Light Tower several hundred yards from the collection site. Small fish collected on these sites had no evidence of *Mytilus* in their digestive tracts.

Comparison of Growth between Virginia and Rhode Island Populations

Results of this study were similar to those of Cooper (1965) in determination of derived growth coefficients and in regressions of morphometric parameters. Calculated L_{mx} values were much higher in Virginia fish, 705 for females, 800 for males, compared to 506 and 664, respectively, for Rhode Island tautog. Calculated L_{mx} (800 mm) as derived from the von Bertalanffy equation is reasonable in comparison with maximum observed TL of 765 mm and yearly growth of older fish. K-values for Virginia tautog indicated that females grew at a slightly faster rate (0.1214 compared to 0.0944) than males. Greater L_{mx} for males, however, resulted in only a small difference in calculated length at age between the sexes. Cooper (1965) also calculated larger K-values for female tautog (0.1519 compared to 0.0911). His study indicates a growth divergence between sexes which favored males after Age 3. Male growth did not surpass female growth in Virginia tautog until Age 11.

The seasonal growth pattern, as reflected by annulus growth increments, is one of rapid somatic growth after spawning. Maximum yearly growth is achieved during the period of July to December. The slower rate of somatic growth during the months of January to June is attributed to decreased feeding activity (Cooper, 1965; Olla et al., 1974) and increased gonadal production (Chenoweth, 1963). Rapid growth of tautog during the first three years is indicated for both northern and southern study areas.

Tautog longevity can only be estimated. Claims of fish "more than half a century old" (Reiger, 1985) seem exaggerated . The average age for tautog in this study was over 7 years, with the oldest age at 21 years. Tautog of 34 years have been noted by Cooper (1965). The current rod-and-reel world record for this species of 21 1/2 lbs was caught in Virginia; therefore, within the constraints of the calculated von Bertalanffy equation and length to weight relationship, a longevity of 30 - 35 years is reasonable for fish in this area.

A comparison of calculated growth from the Von Bertalanffy equations indicates differences in Rhode Island and Virginia tautog populations. Virginia tautog exhibited greater total length at all ages. In comparison of yearly back-calculated growth increments between this study and Cooper (1967) (Table 7), the greatest difference in average yearly increment occurred in the first year. Average incremental growth of Virginia tautog was more than double the length of Rhode Island tautog at the end of the first year. Annual growth increments were similar for all ages after age one, and showed a similar pattern of decline in growth with age.

There are several possible explanations for greater first year growth of Virginia tautog. Firstly, the first annulus may not have been detected. In larger fish the opercle buttress zone radiating from the articular apex did, in some cases, obscure early annuli. However, in instances where the first annulus could not be discerned (less than 5% of the specimens), substitution of the average first annulus increment from all remaining opercles was used for back-calculations of total length. First year length calculations closely matched actual observations of total length in Virginia tautog at Age 1 (Munroe, unpubl.). These results and observations of length at age in Virginia tautog were closely correlated to length-at-age values for young Long Island tautog (Briggs and O'Conner, 1971).

The second, and more plausible, explanation for this observed first year growth difference is that environmentally induced differences in growth rates exist. Both field and experimental observations from northern areas by Olla and coworkers (1974) indicate that young tautog are generally more restricted in seasonal movement than adults and show a decreased activity pattern in water temperature below 10° C. In temperatures below 6° C, small fish seek refuge in crevices or on the bottom and were observed to be covered with silt. This dormancy period extends until warming of the water in the spring (Olla et al., 1979). Onset of colder water temperatures occurs earlier in Rhode Island than in Virginia. Therefore, the longer growing season in the Chesapeake Bay was thus reflected in greater first year growth.

Excluding this first year difference in incremental growth, similarities in the Von Bertalanffy parameters between northern tautog and Virginia tautog indicated that length is an intrinsic growth variable for the species. A comparison of weight at age was also indicative of population differences. Cooper (1967) used eviscerated fish collected in one month to determine the length to weight relationships for Rhode Island tautog; therefore, direct comparison of his results with my data was not feasible. Briggs (1969), however, calculated a length to weight relation from 3,156 whole, unsexed fish collected in New York waters from May until November. This regression,

$$\text{Log } W = -5.992 + 2.916 \text{ Log } L$$

where W = weight (oz) and L = length (mm),

is very similar to that calculated for length to weight (sexes combined) in the present study;

$$\text{Log } W = -4.468 + 2.915 \text{ Log } L$$

where W = weight (g) and L = length (mm).

Assuming growth rates are similar for Rhode Island and Long Island fish, a comparison can be made to Virginia tautog. These results provide both a means to estimate entry age into the fishery and a basis for comparison between populations.

Cooper (1967) indicated that an eviscerated 908 g (2 lb) tautog was considered to be a good fish by rod-and-reel fishermen. Spear fishermen considered an eviscerated 1820 g (4 lb) fish to be a good catch. Uneviscerated Northern tautog (Table 8) weigh 908 g at 7-8 years and 1820 g at 10-11 years. Virginia fish require only 5-6 and 7-8 years, respectively, to attain the same total weight. Although length to weight results are similar between northern and southern areas, weight to age results favor large fish at younger ages in Virginia. These overall differences between populations reflect the relative recent exploitation of the fishery in Virginia and the demographic, environmental, and ecological differences between study areas.

Comparison of Growth between Tautog and other Labrids

There are few published age-growth studies on labrids, undoubtedly because most are tropical and few have commercial or recreational value. Comparisons of growth rates for temperate labrids (ranging from the Eastern Atlantic to the Eastern Pacific) indicated a similar pattern of slow growth and generally extended longevity for these species (Figure 10). I conclude that growth parameters in labrids are not only characteristic of these temperate species, but are comparable throughout the taxa.

Estimates of growth coefficients among taxa can provide insight into ecological strategies. K-values and longevity of other Western Atlantic coastal fishes were compared to the tautog and other labrid species in Table 9. This comparison, which crosses phylogenetic and demographic lines, suggests a K - selection pattern among species occupying substrate limited habitats. These fishes are from a wide spectrum of distantly related taxa and include such species as temperate labrids, coral reef-dwelling snappers and groupers and other outer continental shelf species, such as the burrowing tilefish. These species exhibit growth coefficients of less than 0.22 and are generally long-lived. Conversely, coastal pelagic species exhibit k-values greater than 0.22. Manooch (1979) labeled fish which have k-values ranging from 0.22 - 0.47 as the coastal pelagic cohort. Species with k-values less than 0.22 he grouped as the snapper/grouper cohort. Adopting these categories, I have included the wrasses in the latter cohort.

Management Considerations

Similarities in habitat preference, growth rate, recruitment age and sexual maturity that exist between tautog and the snapper/grouper cohort suggest that some aspects of management strategies could apply to all fisheries in the cohort. Previous studies by Matheson and Huntsman (1984), Manooch and Mason (1984), Moore and Labisky (1984), Harris and Grossman (1985), and Matheson et al., (1986) conclude that intense fisheries for a species exhibiting a slow growth rate and habitat-restricted ecology could detrimentally affect the population. The rapid advances in marine electronics and the growing fishery for tautog in Virginia suggest the need for a management plan.

Any tautog management strategy needs to consider aspects of growth and reproduction. The wide geographic range and habitat type over which this species is found add complexity to seasonal patterns of migration, spawning and social behavior. Musick and Mercer (1977) concluded that heavy fishing pressure on the hermaphroditic black sea bass, Centropristes striata, may impact on reproduction through changes in sex ratio. Further, in some fishes, sex-reversal may be behaviorally dependent upon sex-ratio (Shapiro and Lubbock 1980). Since directed fishing pressure through selection of larger individuals impacts on the sex-ratio of tautog and, therefore, on reproductive success, it is important that the reproductive strategies of tautog be well understood. Research is also needed on the relative reproductive contributions of inshore and offshore cohorts and early life history and larval ecology before management options can be fully explored.

Our present knowledge limits management recommendations that can be made at this time. Foremost in the enhancement of the Virginia tautog population is the continued development of artificial reefs. Artificial reef projects in Virginia have been highly successful in increasing both fishing success and usable substrate for the species (Feigenbaum and Blair, 1986). The value of artificial reefs is twofold. First, reef development would increase suitable habitat for tautog and associated reef species. This is especially important in Virginia since suitable substrate appears to be a limiting factor. Secondly, placement of these structures over a wide area would disperse fishing pressure since competition for fishing space on available isolated wrecks can at times be intense. Dispersion of artificial structures could reduce this competition among fisherman and consequently diminish pressure on the species. Additionally, development and management of reef areas allowing for periodic closing to fishing would provide refuge for the tautog and associated reef fishes. Further research into the habits of tautog fishermen and the migration of tautog in Virginia would help maximize the benefit of these projects.

Figure 1. Station locations from which tautog were sampled.

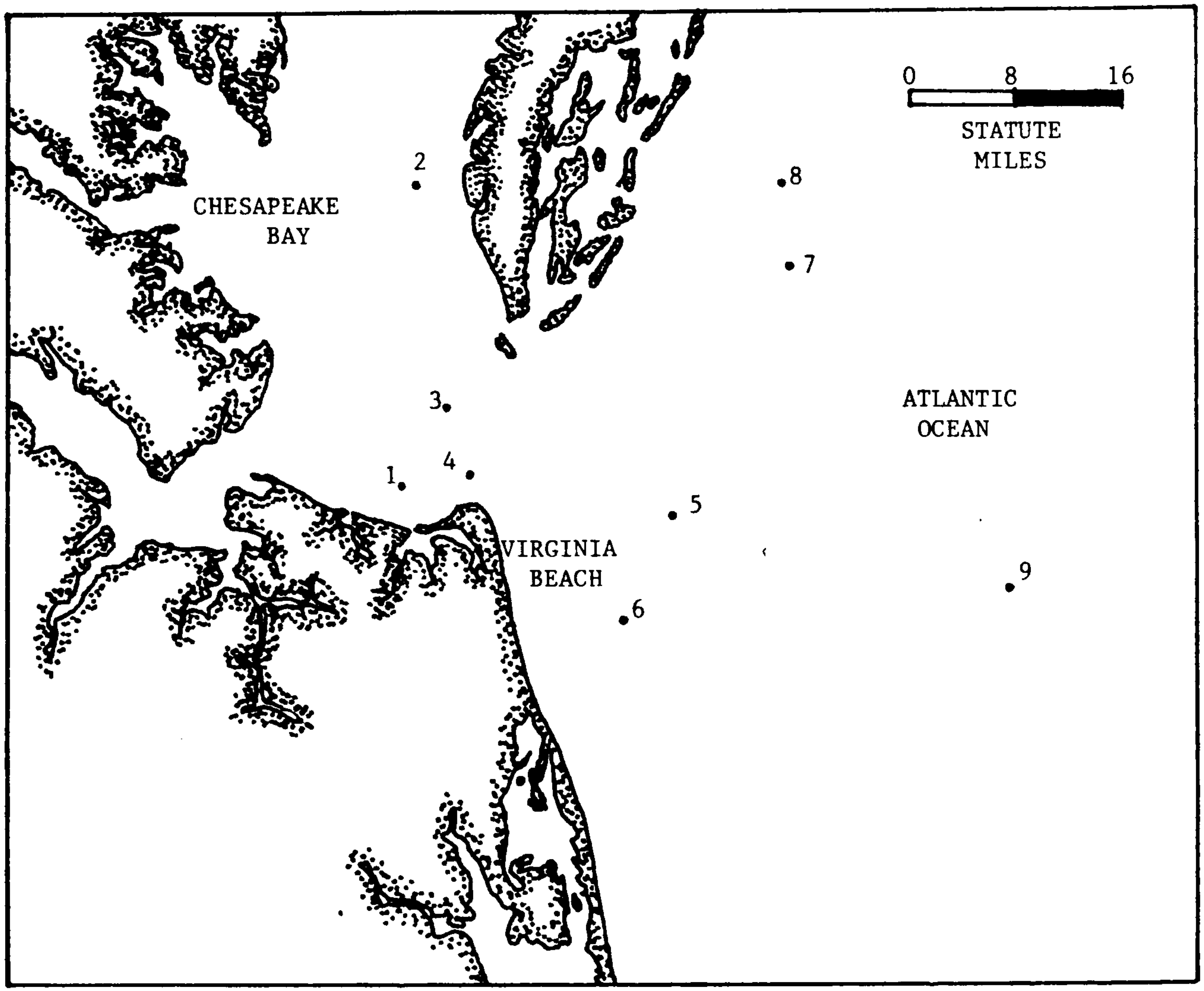

0 8 16
STATUTE
MILES
CHESAPEAKE
BAY
ATLANTIC
OCEAN
VIRGINIA
BEACH
1
2
3
4
5
6
7
8
9

Figure 2. Representation of left tautog opercle, Age 5.

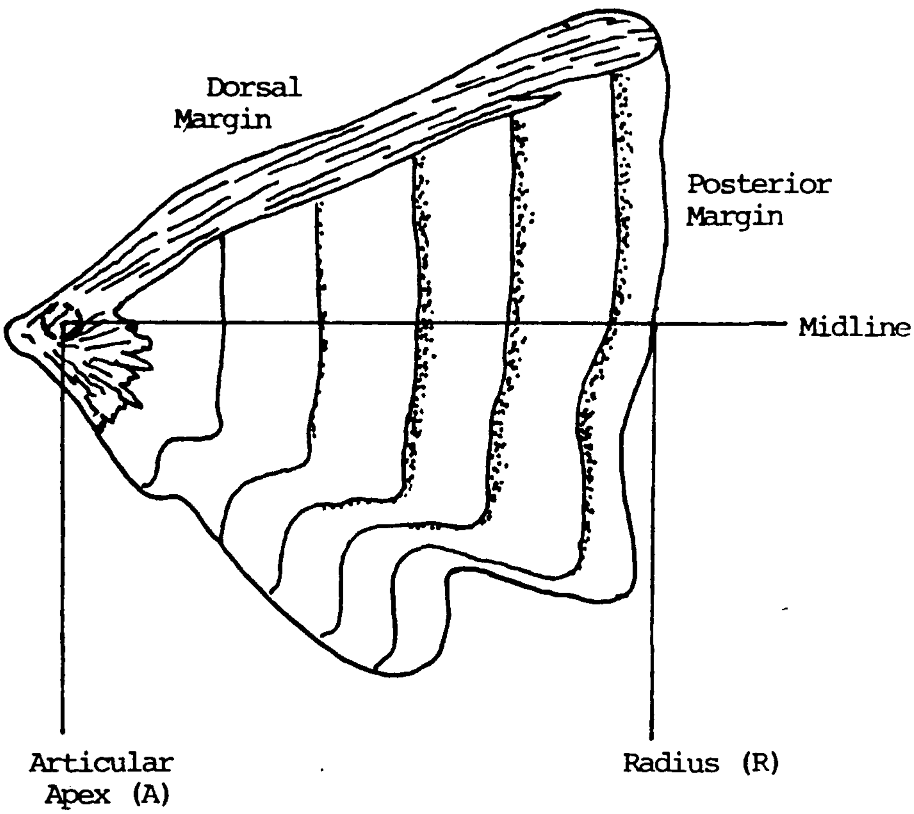

Dorsal
Margin
Posterior
Margin
Midline
Articular
Apex (A)
Radius (R)

Figure 3. Length to weight relation for male tautog in Virginia.

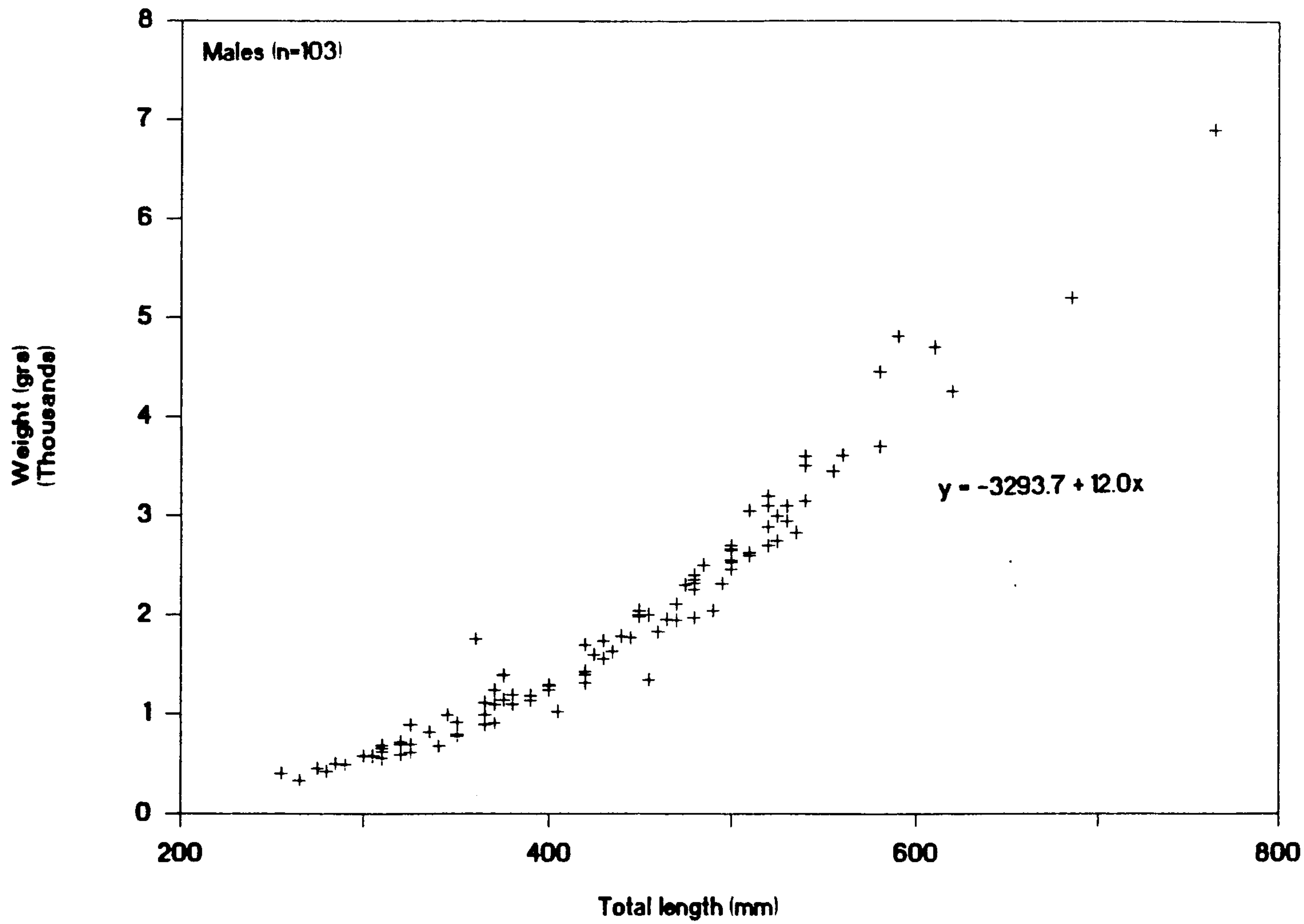

Males (n=103)
y = -3293.7 + 12.0x
Weight (grs)
(Thousands)
0
1
2
3
4
5
6
7
8
200
400
600
800
Total length (mm)

Figure 4. Length to weight relation for female tautog in Virginia.

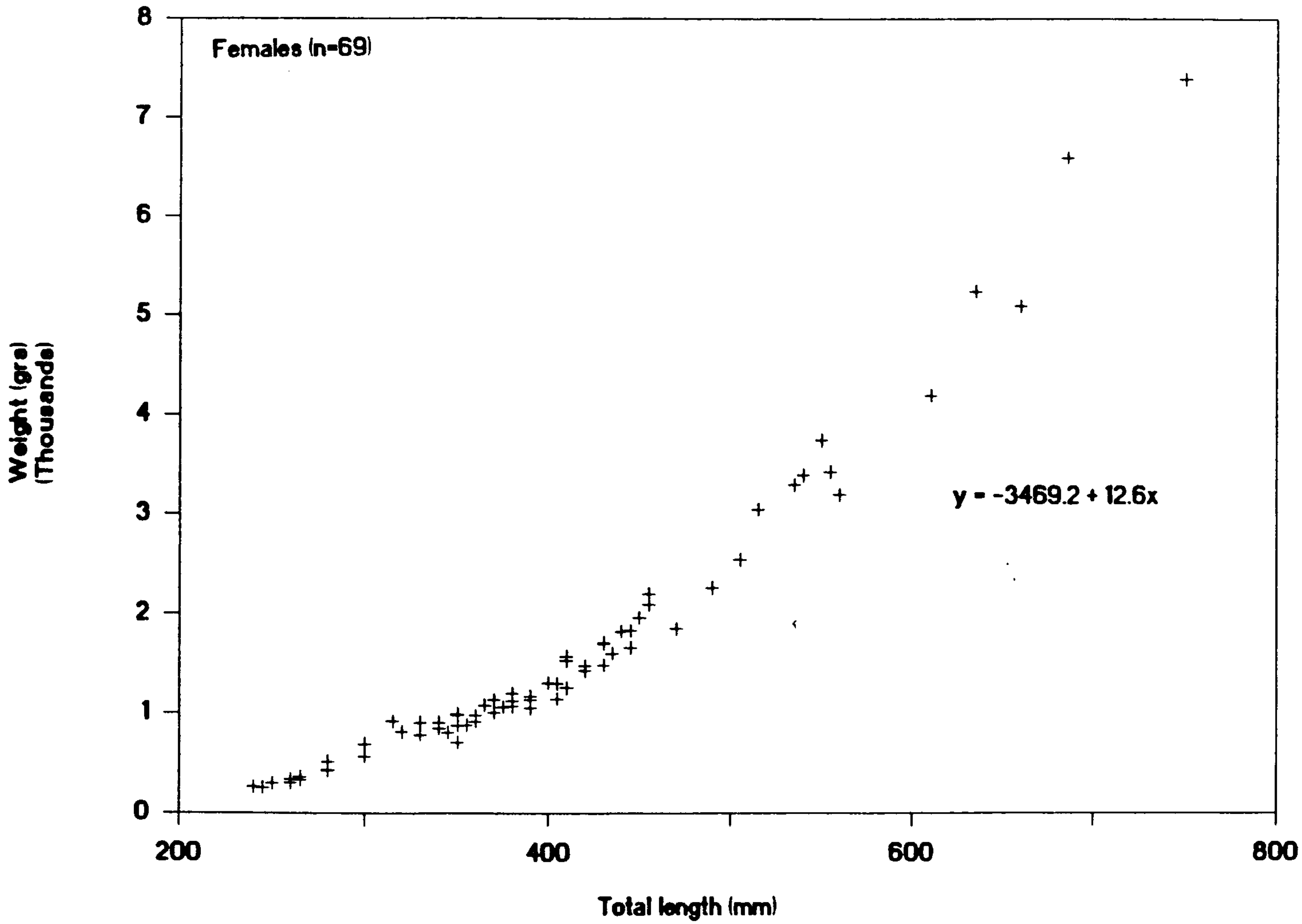
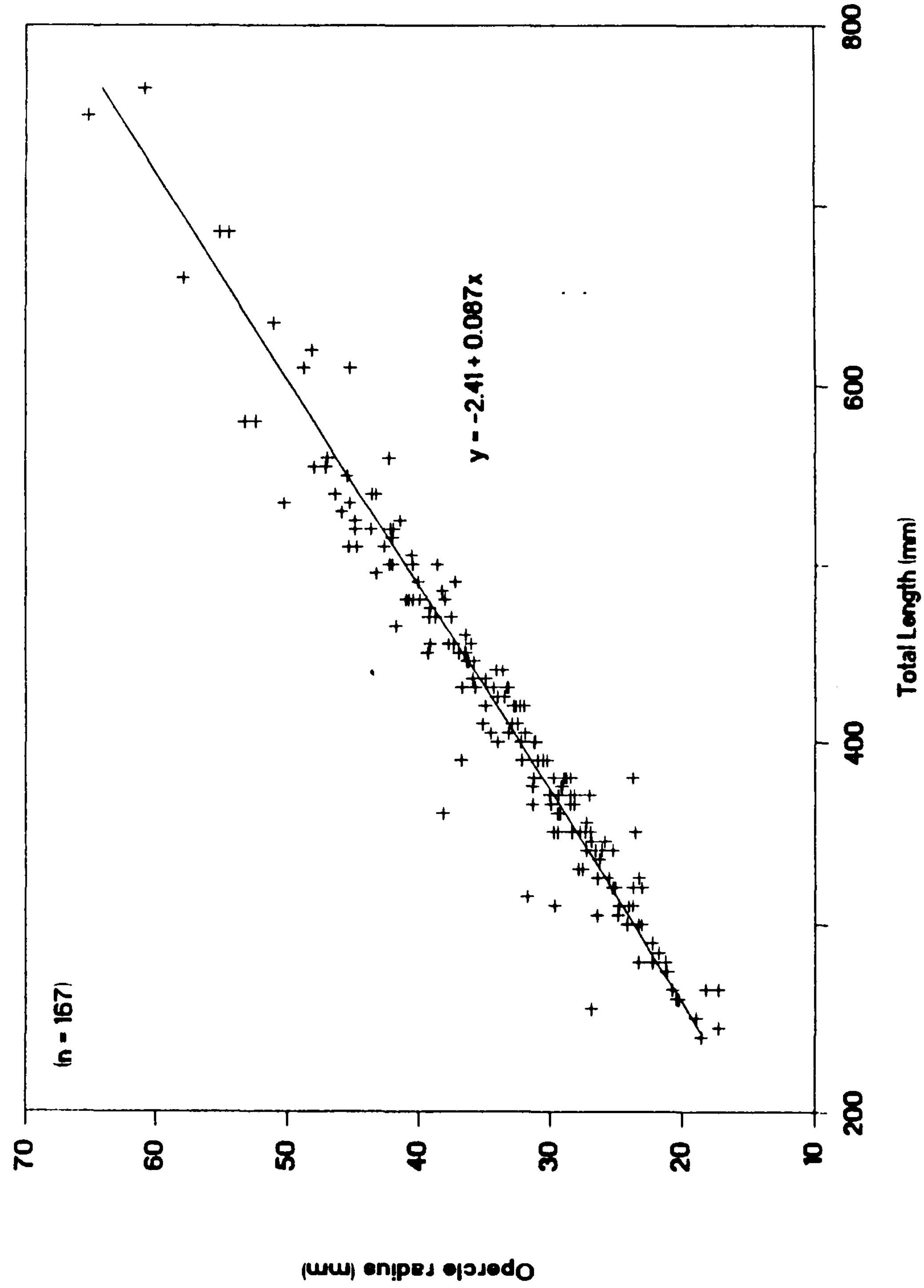
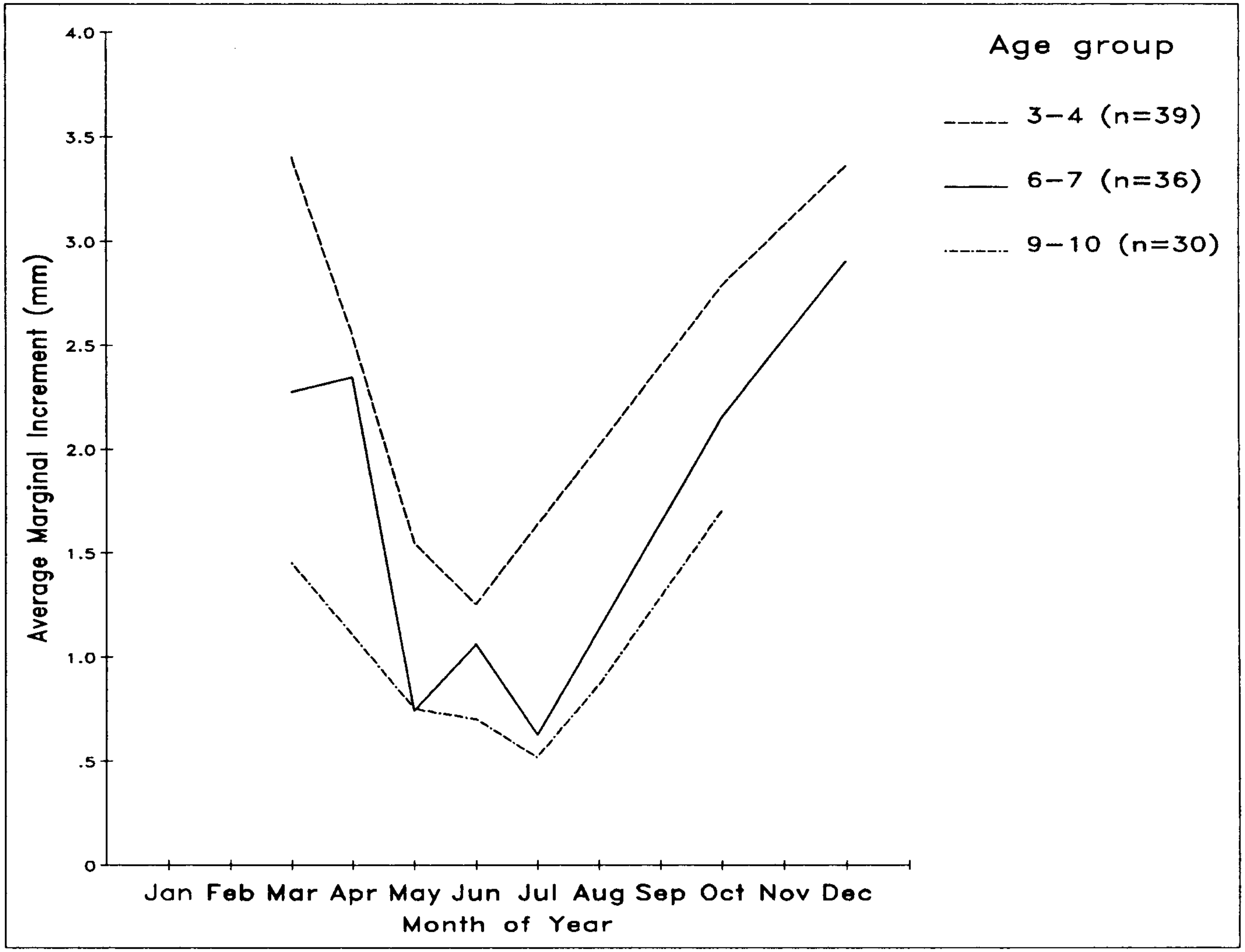

Females (n=69)
y = -3469.2 + 12.6x
Weight (grs)
(Thousands)
Total length (mm)
0
1
2
3
4
5
6
7
8
200
400
600
800

Figure 5. Relation of opercle radius (mm) against total length (mm) for tautog sampled in Virginia (1984 - 1986).



(n = 167)
y = -2.41 + 0.087x
Total Length (mm)
Opercle radius (mm)
200
400
600
800
10
20
30
40
50
60
70

Figure 6. Incremental growth of opercle since last annulus formation (mm) for tautog age groups 3-4, 6-7 and 9-10 by month of capture.



Age group
3–4 (n=39)
6–7 (n=36)
9–10 (n=30)
Average Marginal Increment (mm)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month of Year

Figure 7. Von Bertalanffy estimates of total length (mm) against age (yr) for male and female tautog in Virginia.

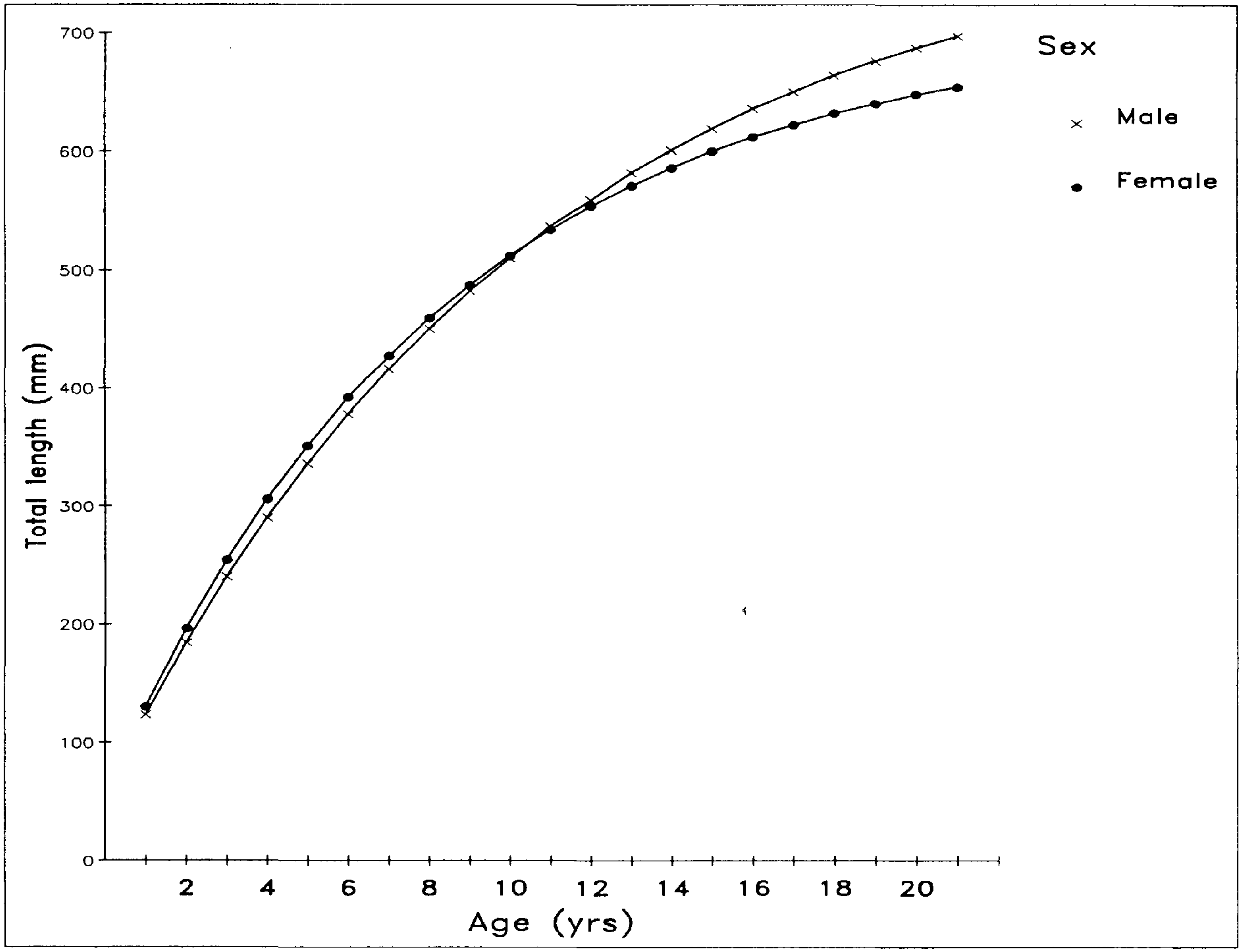

Sex
Male
Female
Total length (mm)
0
100
200
300
400
500
600
700
Age (yrs)
2
4
6
8
10
12
14
16
18
20

Figure 8. Von Bertalanffy estimates of annual incremental growth (mm) against age (yr) for male and female tautog in Virginia.

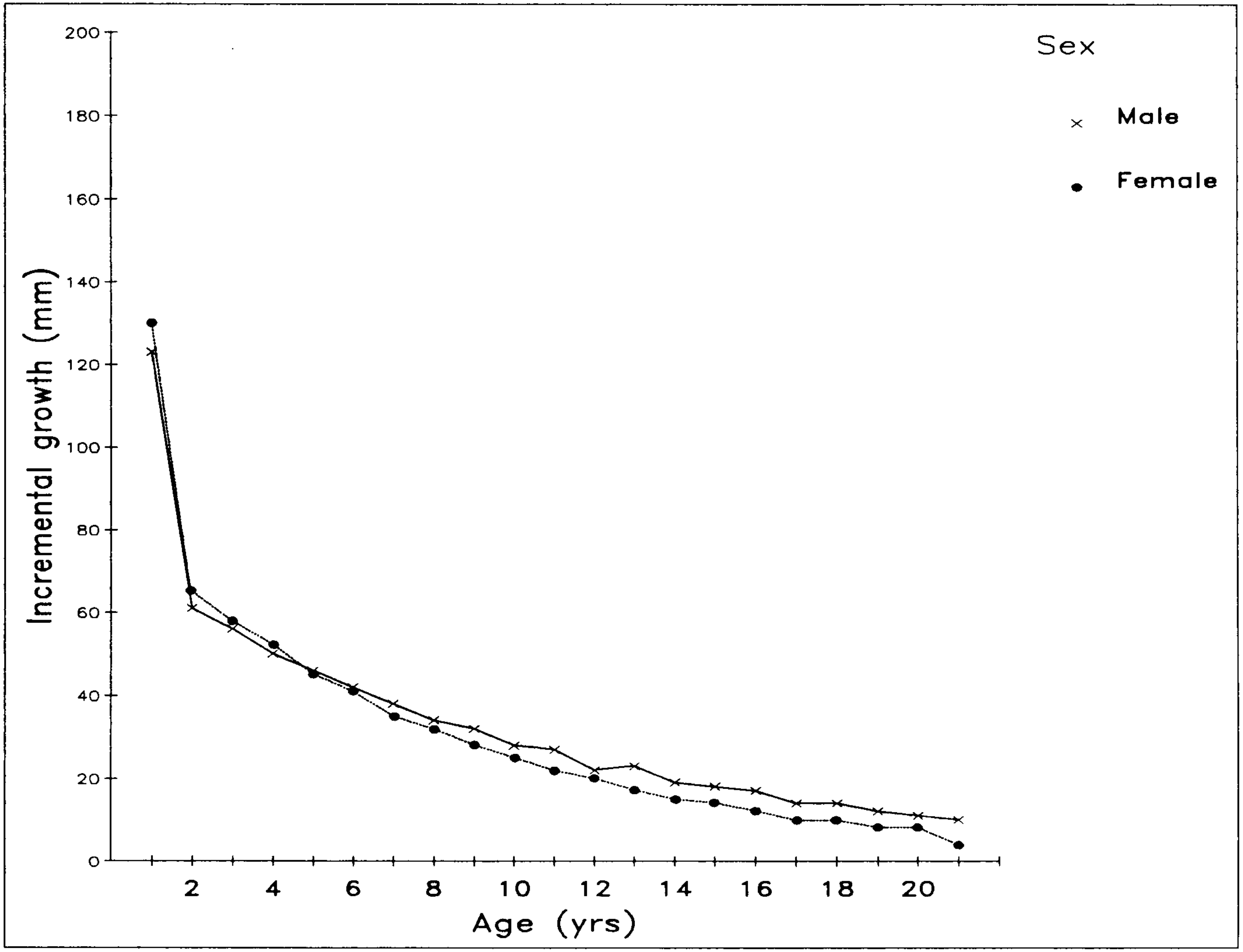

Sex
Male
Female
Incremental growth (mm)
Age (yrs)
0
20
40
60
80
100
120
140
160
180
200
2
4
6
8
10
12
14
16
18
20

Figure 9. Gonadosomatic Index (GSI) for female tautog by month of capture (1984 - 1986).

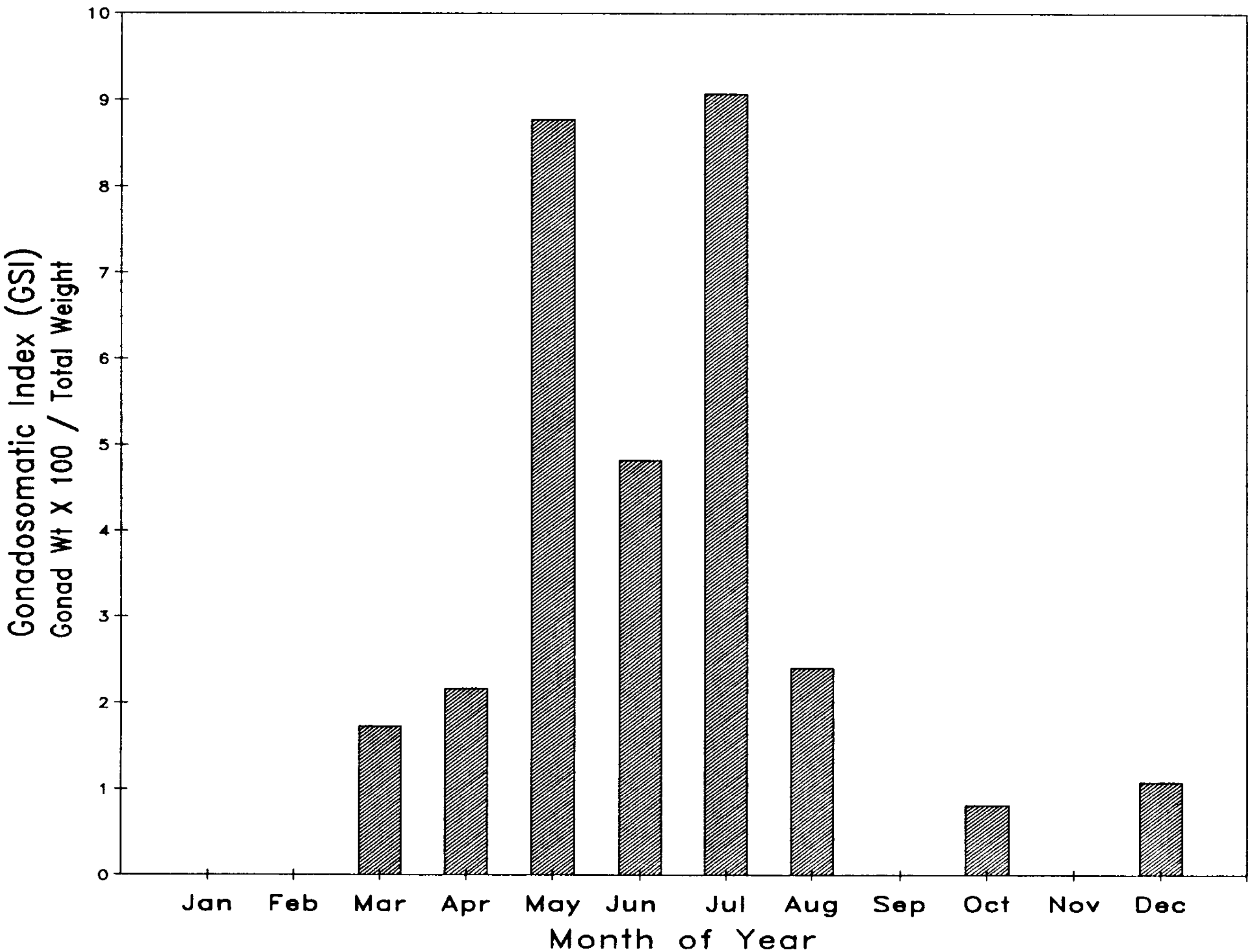
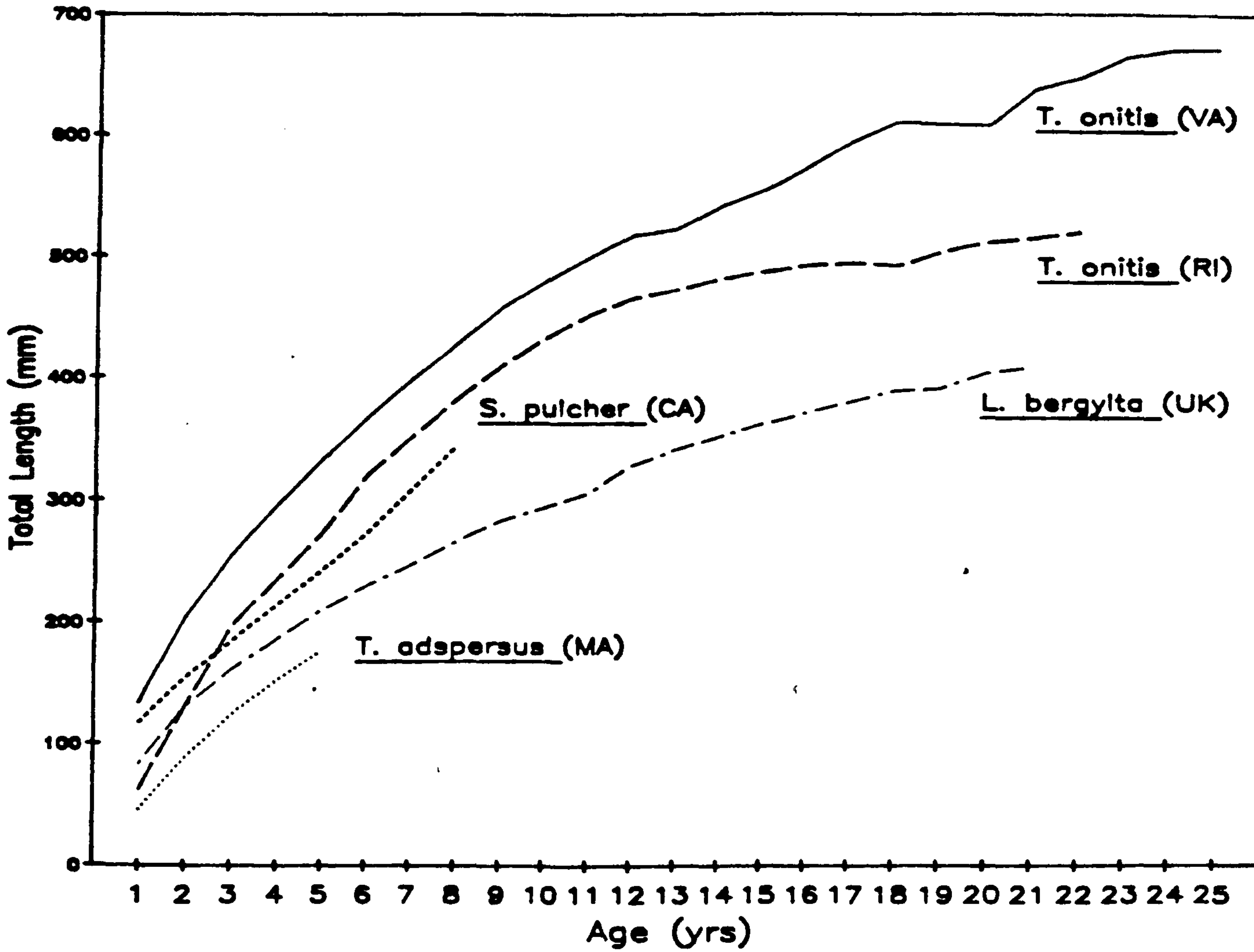

Gonadosomatic Index (GSI)
Gonad Wt X 100 / Total Weight
0
1
2
3
4
5
6
7
8
9
10
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month of Year

Figure 10. Growth curves of the temperate labrids _Semicossyphus pulcher_, _Tautogolabrus adspersus_, _Labrus bergylta_, and _Tautoga onitis_.



Back calculated growth curves of temperate Labrids.

Table 1. Summary of information for nine collecting stations from which tautog were sampled.

Station #	Depth(m)	Location
1	2-11	South Island Chesapeake Bay Bridge Tunnel ($36^{o}58.0'$N $76^{o}07.0'$W)
2	12	Cape Charles Artificial Reef ($37^{o}14.0'$N $76^{o}04.0'$W)
3	2.5-11	Third Island Chesapeake Bay Bridge Tunnel ($37^{o}02.0'$N $76^{o}04.3'$W)
4	17	Cape Henry Wreck ($36^{o}57.3'$N $76^{o}00.5'$W)
5	14-20	Chesapeake Light Tower Reef ($36^{o}54.0'$N $75^{o}43.0'$W)
6	18	V-Buoy (Tiger Wreck) ($36^{o}44.3'$N $75^{o}46.3'$W)
7	18	Doxy Girl Wreck ($37^{o}08.3'$N $75^{o}35.3'$W)
8	21	Birch Lake Wreck ($37^{o}11.3'$N $75^{o}16.3'$W)
9	25	Frances E. Powell Wreck ($36^{o}48.3'$N $75^{o}24.0'$W)

Table 2. Comparison of age estimates using otoliths and opercles from tautog.

Specimen Number	Age (yrs) Opercle	Otolith
1	12	10?11
2	11	8?9
3	6	6
4	6	5?6
5	9	9
6	6	5
7	8	9?8
8	8	9?8
9	7	7
10	8	6?7
11	6	6?5
12	7	7
13	10	8?9
14	7	7?6
15	9	9?8
16	8	8?7
17	10	11?10
18	5	6?5
19	9	9?10
20	4	5
21	5	5?6
22	7	6?7
23	5	5
25	3	3
31	3	2
32	2	2
63	10	9?10

Table 3. Back-calculated total length (mm) of female tautog from Virginia, (1984-1986).

Age Group	No. of fish	Length at capture	Total calculated length at formation of nth annulus 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
II	3	245	124	217																			
III	9	284	119	197	252																		
IV	8	347	125	218	287	329																	
V	13	363	125	203	254	310	347																
VI	7	422	126	201	261	308	363	403															
VII	9	404	119	182	240	278	315	355	383														
VIII	4	429	126	205	255	299	330	364	398	426													
IX	5	459	132	202	254	298	340	366	392	416	443												
X	3	535	146	224	274	318	365	394	426	455	499	528											
XI	2	557	136	182	274	345	400	442	474	495	515	528	548										
XII	-	-	-	-	-	-	-	-	-	-	-	-	-	-									
XIII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
XIV	1	635	167	239	282	354	435	484	506	521	541	562	581	600	619	635							
XV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
XVI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
XVII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
XVIII	3	614	126	174	220	254	287	321	352	379	407	434	462	488	509	536	557	578	592	608			
XIX	1	685	151	232	287	339	399	428	454	466	484	516	541	574	593	614	632	647	662	677	682		
XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXI	1	660	148	185	224	277	324	368	404	451	487	513	536	555	569	579	594	600	605	627	637	647	655
Average calculated increment			134	70	55	50	46	38	28	30	31	32	20	19	20	18	3	14	12	17	23	-13	8
Sum of calculated increments			134	204	259	309	355	393	421	451	482	514	534	553	573	591	594	608	620	637	660	647	655

Table 4. Back-calculated total length (mm) of male tautog from Virginia, (1984-1986).

Age Group	No. of fish	Length at capture	Total calculated length at formation of nth annulus																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
II	3	290	168	261																			
III	11	309	118	213	270																		
IV	11	347	134	218	282	328																	
V	9	378	117	191	256	318	358																
VI	10	357	120	181	230	270	305	338															
VII	10	416	135	207	258	292	335	372	407														
VIII	7	444	132	202	265	309	342	375	411	438													
IX	14	483	140	206	263	311	352	387	418	448	472												
X	9	516	137	207	261	309	351	386	418	446	479	508											
XI	4	509	130	197	258	302	337	377	407	434	458	478	497										
XII	7	550	126	186	237	295	333	373	411	443	470	498	520	541									
XIII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
XIV	1	555	133	180	221	289	337	369	412	440	472	493	513	530	545	552							
XV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
XVI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
XVII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
XVIII	2	724	167	219	257	290	327	366	410	448	485	525	557	589	630	659	681	700	711	718			
XIX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
XXI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Average calculated increment			135	70	50	46	37	33	41	30	31	27	22	31	35	18	75	19	11	7	-	-	-
Sum of calculated increments			135	205	255	301	338	371	412	442	473	500	522	553	588	606	681	700	711	718	-	-	-

Table 5. Comparison of average observed length (mm) at capture against back-calculated and Von Bertalanffy estimates for male and female tautog in Virginia.

Age	L_t Males (obs)	(calc)	(V.B.)	L_t Females (obs)	(calc)	(V.B.)
1	-	135	123	-	134	130
2	290	205	184	245	204	196
3	309	255	240	284	259	254
4	347	301	290	347	309	306
5	378	338	336	363	355	351
6	357	371	378	422	393	392
7	416	412	416	404	421	427
8	444	442	450	429	451	459
9	483	473	482	459	482	487
10	516	500	510	535	514	512
11	509	522	537	557	534	534
12	550	553	559	-	553	554
13	-	588	582	-	573	571
14	555	606	601	635	591	586
15	-	681	619	-	594	600
16	-	700	636	-	608	612
17	-	711	650	-	620	622
18	724	718	664	614	637	632
19	-	-	676	685	660	640
20	-	-	687	-	647	648
21	-	-	697	660	655	654

Table 6. Chi-square analysis of sex-ratio for Virginia tautog by total length (mm).

Standard length (mm)	No. Males	No. Females	Male:Female Ratio	X^2
0-100	-	-	-	-
101-200	22	19	1.16:1	0.2195
201-300	101	80	1.26:1	2.4365
301-400	92	70	1.31:1	2.9876
401-500	80	47	1.70:1	8.5748*
501-600	17	2	8.50:1	11.8421*

* Significant (X^2 .01; 1 d.f.)

Table 7. Comparison of Back-calculated annual growth for Cooper's (1965) Rhode Island tautog against Virginia tautog.

Age	Males				Females			
	Back-calculated Tot. Length (mm)		Avg. Yearly Increment		Back-calculated Tot. Length (mm)		Avg. Yearly Increment	
	VA	RI	VA	RI	VA	RI	VA	RI
1	135	61	135	61	134	63	134	63
2	205	132	70	71	204	130	70	67
3	255	201	50	69	259	193	55	63
4	301	249	46	48	309	239	50	46
5	338	295	37	46	355	279	46	40
6	371	330	33	35	393	310	38	31
7	412	361	41	31	421	340	28	30
8	442	396	30	35	451	368	30	28
9	473	427	31	31	482	393	31	25
10	500	451	27	24	514	415	32	22
11	522	471	22	20	534	433	20	18
12	553	484	31	13	553	447	19	14
13	588	490	35	6	573	457	20	10
14	606	499	18	9	591	464	18	7
15	681	510	75	11	594	466	3	2
16	700	517	19	7	608	469	14	3
17	711	525	11	8	620	464	12	-5
18	718	531	7	6	637	466	17	2
19					660	467	23	1
20					647	477	-13	10
21					655	474	8	-3

Table 8. Comparison of total weight (g) at age (yr) for northern tautog against Virginia tautog.

Northern			Virginia		
Tot length (mm)	Wt (gs)	Age (yrs)	Tot length (mm)	Wt (gs)	Age (yrs)
150	77	2	150	75	1
175	119	2	175	118	2
200	173	3	200	174	2
225	247	4	225	245	2
250	335	4	250	333	3
275	439	5	275	439	3
300	567	5	300	566	4
325	717	6	325	715	5
350	890	7	350	887	5
375	1089	8	375	1085	6
400	1315	9	400	1309	6
425	1568	10	425	1562	7
450	1854	11	450	1846	8
475	2169	12	475	2161	9
500	2520	14	500	2509	10
525	2906	16	525	2892	11
550	3328	18	550	3313	12
575	3788	>20	575	3771	13
600	4289	>20	600	4269	14
625	4831	>20	625	4808	15
630	4941	>20	630	4921	>15

Table 9. Growth coefficients (k-values) and longevity of selected labrids and other Western Atlantic coastal fishes.

Species	Source	Age (yrs)	L_{mx}	K
Snowy grouper, (Epinephelus niveatus)	Matheson & Huntsman (1984)	17	1255	0.07
Tautog, (Tautoga onitis)	Hostetter (1987)	25	800	0.09-0.12
Ballan wrasse, (Labrus bergylta)	Dipper et al. (1977)	29	405	-
Cal. sheephead, (Semicossyphus pulcher)	Warner (1975)	>20	800	-
Lane snapper, (Lutjanus synagris)	Manooch & Mason (1984)	10	501	0.13
Speckled hind, (E. Drummondhayi)	Matheson & Huntsman (1984)	15	967	0.13
Mutton snapper, (Lutjanus analis)	Mason & Manooch (1985)	14	862	0.15
Tilefish, (L. Chamaelonticeps)	Turner et al. (1983)	35	960	0.16
Red snapper, (L. Campechanus)	Nelson & Manooch (1982)	16	975	0.16
Scamp, (Mycteroperca phenax)	Matheson et al. (1984)	21	985	0.17
Cunner, (T. adspersus)	Serchuk & Cole (1974)	6	285	0.20
Black sea bass, (Centropristis striata)	Wenner et al. (1986)	10	341	0.23
Bluefish, (Pomatomas saltatrix)	Wilk (1977)	9	-	0.23
Blue runner, (Caranx crysos)	Goodwin & Johnson (1986)	11	412	0.35
King mackerel, (Scomberomorus cavalla)	Nommura & Rodriques (1967)	14	-	0.35
Atlantic menhaden, (Brevoortia tyrannus)	Schaaf & Huntsman (1972)	-	-	0.39
Yellowfin tuna, (Thunnus albacares)	Leguen & Sahagawa (1973)	-	-	0.42

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