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Comparison of scales and otoliths for determining age and growth of the alewife (*Alosa pseudoharengus*, Wilson)

Douglas Wayne Lipton

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COMPARISON OF SCALES AND OTOLITHS FOR DETERMINING
AGE AND GROWTH OF THE ALEWIFE (ALOSA PSEUDOHARENGUS, WILSON)

A Thesis

Presented to

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

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Arts

by

Douglas Wayne Lipton

1979

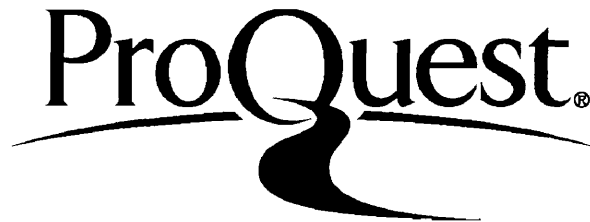
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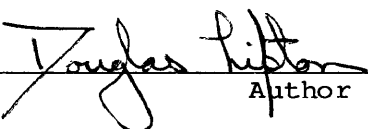
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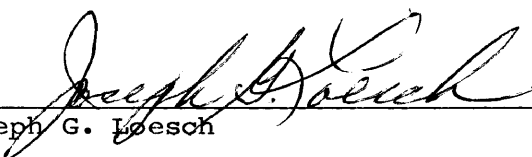
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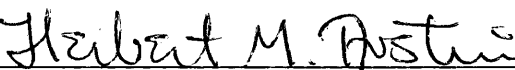
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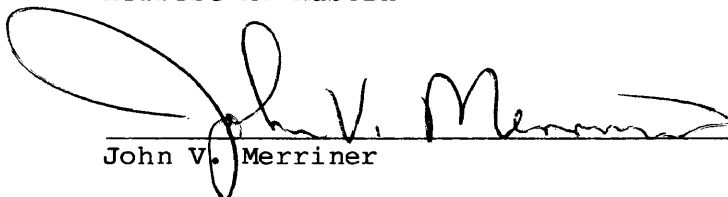
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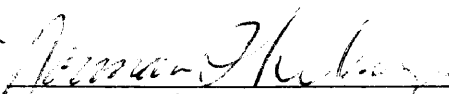
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ABSTRACT

Otoliths were validated for determining the age of alewives, Alosa pseudoharengus, in Virginia. Reader agreement was 83% for otoliths and 77% for scales. Agreement was poor (45%) between otolith and scale ages. The age structure established from otoliths was younger than that from scales.

Mean observed lengths-at-age from the two ageing methods were similar. Fork length on otolith and scale radius regressions were linear. Walford lines based on back-calculated lengths were significantly different for males and females when otoliths were used for ageing but not when scales were used.

Von Bertalanffy growth curves were computed for males and females from back-calculations by both ageing methods. Total length-fork length and weight-length relationships were calculated.

It was concluded that otoliths were more precise and efficient than scales for age and growth studies of Virginia alewives because of the inherent reading problems of scales (erosion, regeneration, etc.) and scale loss or damage sustained in the commercial fishery.

COMPARISON OF SCALES AND OTOLITHS FOR DETERMINING
AGE AND GROWTH OF THE ALEWIFE (ALOSA PSEUDOHARENGUS, WILSON)

INTRODUCTION

The alewife Alosa pseudoharengus (Wilson), an anadromous member of the family Clupeidae, ranges from Nova Scotia and the Gulf of St. Lawrence to North Carolina (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953).

In Virginia, the alewife and blueback herring Alosa aestivalis (Mitchill) comprise the river herring fishery. The fishery operates in Chesapeake Bay and its tributaries during the anadromous spawning runs from about mid-March through June. The commercial catches of the two species are not separated, and landings are reported as alewives by the National Marine Fisheries Service, Division of Statistics and Market News. Pound nets are the principal gear used in the harvest, but gill nets, fyke nets, drift nets, haul seines, and hand-held dip nets are also employed.

The general trend in Virginia alewife landings has been downward since 1969 and the 1977 catch of 630 metric tons was only 34% of the previous low in 1976 (Loesch et al. 1977).

Management and monitoring of a fishery requires knowledge of the age structure and growth of the fish stock. Scales have been used to back-calculate alewife lengths in Maine (Havey 1961), Connecticut (Marcy 1969), New Brunswick (Messieh 1977), and North Carolina (Kornegay 1978). Investigators at the Virginia Institute of Marine Science (VIMS) have

collected alewife scales for ageing from the commercial catch since 1965 (Joseph and Davis 1965; Hoagman et al. 1973; Loesch and Kriete 1976); however, lengths were not back-calculated because scales could not consistently be collected from a given body location (i.e., a "key region"). The pumping or brailing of fish from pound nets into vessels and the subsequent dock-side unloading results in a large scale loss.

Some common problems with using scales for ageing and back-calculation of length reported by numerous investigators are: 1) mucus can cause scales of one fish to stick to another; 2) lost scales and their subsequent regeneration may invalidate readings (Messieh and Tibbo 1970; Carlander 1974); 3) spawning checks may erode past previous annuli causing an underestimate of age and an overestimate of the growth rate (Berg and Grimaldi 1967); 4) the presence of false annuli may cause an overestimate of age and thus, an underestimate of the growth rate (June and Roithmayr 1960; Berg and Grimaldi 1967; Tsimenides 1970); and 5) reabsorption of recent annuli may occur when growth conditions are poor (Buchholz and Carlander 1963).

Many researchers have turned to otoliths to age fish because of the many difficulties when relying on scales to determine age and growth. Mosher and Eckles (1954) found otoliths to be as precise as scales in determining age of the Pacific sardine, Sardinops sagax. Grande (1964) found otoliths of the brook trout, Salvelinus fontinalis, more precise and easier to read than the scales. Watson (1964) working mainly with young Clupea harengus, validated ageing of this species by otoliths; however, Messieh and Tibbo (1970) concluded that scales were more accurate than otoliths especially for the older herring. Eggleston (1975) found that otoliths were easier to interpret and had more annuli

than scales when ageing old kahawai, Arripis trutta.

Alewives have been aged from otoliths (Netzel and Stanek 1966; Norden 1967; Messieh 1977). Kornegay (1978) used scales and otoliths to age and back-calculate lengths of alewives and blueback herring. He found that the relationship between fork length and scale radius was linear, but the fork length and otolith radius relationship was non-linear. Messieh (1975) found a linear relationship between body length and otolith size for Clupea harengus. Jonsson and Stenseth (1977) found otoliths to be superior to scales for both ageing and length estimation of cod, Gadus morhua. Powles and Kennedy (1967) used otoliths to age and estimate growth of Nova Scotian greyscale, Glyptocephalus cynoglossus. Bailey et al. (1977) used otoliths to age and back-calculate lengths of capelin, Mallotus villosus. Age and growth of summer flounder, Paralichthys dentatus, were determined from otoliths, and the relationship of otolith radius to total length was found to be linear (Smith and Daiber 1977).

The objectives of this study were: 1) to age and back-calculate lengths of Virginia alewives; 2) determine growth functions; and 3) assess the efficiency of using otoliths relative to using scales.

MATERIALS AND METHODS

Data Source

A total of 710 alewives was collected from the Rappahannock River pound-net fishery from early April to early July, 1977. Only fish caught above river kilometer 16 (mile 10) were collected on the

assumption that these fish were committed to the river for spawning. Spawning alewives in Virginia are mostly age 4 or older. To avoid the inherent error in growth analysis introduced by a limited size range (Whitney and Carlander 1956), young fish (ages 1 to 4) were obtained from trawl samples in February offshore of the mouth of Chesapeake Bay. In addition young-of-the-year alewives were caught in the Rappahannock River in August, 1978.

Sample data recorded were date, location, type of gear, sex, fork and total length to the nearest mm, and weight with and without gonads to the nearest 0.1g.

Scales

Alewife scales closely resemble the scales of American shad Alosa sapidissima (Wilson) as described by Cating (1953). The major features on the anterior portion of these cycloid scales, which follow along the periphery of the scale, are a freshwater zone, annuli, and spawning checks (Fig. 1). Running laterally across the annuli are a baseline and transverse grooves.

Scales were removed from the key region defined by Marcy (1969) as the left side above and below the lateral line at the level of the vent. When scales were taken from an area other than the key region, it was recorded on the coded scale envelope used for scale storage so that these scales would not be used in back-calculations. Five scales or less were cleaned with warm water and then pressed on a clear acetate card in a Carver Laboratory Press at approximately 20,000 p.s.i. at 80 C for two minutes.

Scale impressions were examined with an Eberbach Scale Projector

at 40X magnification. Age was determined by the method of counting the number of annuli and spawning checks and adding a year for the outer edge (Cating 1953). Distances to annuli were measured along a line from the center of the baseline to a point on the anterior periphery (Marcy 1969). The author and a co-worker independently aged each scale.

Otoliths

The three otoliths in the labyrinth of the ear of bony fishes are composed of calcium carbonate crystals in a network of organic material (Williams and Bedford 1974). The largest of the three otoliths, the sagitta, is generally used for ageing, and is the otolith referred to in this study. The otolith is oval in appearance with an opaque nucleus surrounded by alternating concentric rings of hyaline and opaque material (Fig. 2). The opaque material is laid down from late winter to late fall and the hyaline material is laid down during the winter season of slow growth and reduced feeding.

Otoliths were removed by slicing through the head about 3 mm behind the eye. The brain and semicircular canals were lifted up and out to expose the otoliths, which were then removed with forceps and stored dry in a one dram vial.

Otoliths were placed in glycerin in a petri dish with a black background, and examined at 50X magnification under a dissecting microscope with reflected light. Age was determined by counting the number of hyaline (winter) zones. The distance to the outer edge of each winter zone was measured with an ocular micrometer along the axis from the nucleus to the posterior edge. Two workers independently examined each otolith.

Data Analysis

All disagreements on the scale or otolith age were reconciled by a third reading. The number of disagreements between the two workers was tested for independence from the ageing method using a chi-square test of independence. Similar statistical analysis was used to test independence of age frequency from the ageing method for the adult Rappahannock River alewives.

Back-calculations of fork length were computed from the modified "Dahl-Lea" equation:

$$L_t = C + (R_t/R_c) (L_c - C)$$

where L_t = length at age t , R_t = scale or otolith radius at capture, L_c = fork length at capture, and C = the correction constant determined from the Y-intercept of the regressions of scale radius and otolith radius on fork length. The regressions of scale and otolith radius on fork length were fitted for each sex and tested for uniqueness by analysis of covariance. Sex data were pooled if no significant difference was found.

Estimates of fork length-at-age were obtained by the following methods: 1) mean observed length-at-age as determined by scales; 2) mean observed length-at-age as determined by otoliths; 3) mean back-calculated length-at-age as determined by scales; and 4) mean back-calculated length-at-age as determined by otoliths.

Mean observed lengths-at-age (methods 1 and 2, above) were tested for significant differences between methods by a t-test. An approximation of t (t') was computed if an F-test of the variances was significant ($P < 0.01$). Only ages with sample size greater than 10 were

compared.

Mean back-calculated lengths-at-age (methods 3 and 4, above) were compared by analysis of covariance of the Walford (1946) lines (i.e., the regressions of length at age $t+1$ on length at age t). Before methods 3 and 4 were compared, comparisons of the Walford lines by sexes were made to see if these data could be pooled. The slope of the Walford line (e^{-K}) and its intercept with a 45° diagonal from the origin are often used to estimate the parameters K and L_∞ , respectively of the von Bertalanffy growth equation:

$$l_t = L_\infty (1 - e^{-K(t-t_0)})$$

where l_t = length at time t , L_∞ = mean asymptotic length, K = a growth coefficient, and t_0 = a hypothetical age at which the fish would have zero length if growth always followed the equation. Significantly different Walford lines would be an indication that the von Bertalanffy growth curves also differ. Fabens' (1965) computer program was used to fit back-calculated lengths-at-age based on more than 10 observations to the von Bertalanffy growth curve.

The weight-length relationship assumed was:

$$W = aL^b$$

where W = weight without gonads, L = fork length, and a and b are unknown parameters. \log_e transformation to linearity was used to estimate the parameters, so the relationship becomes:

$$\log_e W = \log_e a + b \log_e L$$

from which a and b were estimated. Uniqueness of the weight-length relationships for sexes was tested for significance by analysis of covariance.

The linear regression of total length on fork length was fitted to

the data by sex and tested for uniqueness by analysis of covariance.

Statistical significance is reported in terms of the probability (P) due to chance of observing a deviation \geq that observed.

RESULTS

Age Determinations

Otoliths of young-of-the-year alewives collected in the Rappahannock River in August had a nucleus and a wide opaque zone, but no hyaline zones (Fig. 3); however, otoliths of young-of-the-year alewives caught offshore in February had, in addition, a hyaline zone on the outer edge (Fig. 4). These findings validate the use of otolith hyaline zones as annuli.

A total of 720 otoliths and 700 scale samples were aged and measured. One pair of crystalline otoliths and 52 scale samples were unreadable. The two readers agreed on 77% of the scale ages and on 83% of the otolith ages (Table 1). A chi-square analysis (Table 2) indicated that the number of agreements and disagreements was not independent of the method of ageing ($P < 0.01$), which indicates that reader agreement for otoliths was significantly greater than for scales. Of the total number of otoliths read, 113 (15.7%) were one-year differences, 10 (1.4%) were two-year differences and 1 (0.1%) was a three-year difference. Similarly for scales, 154 (22%) were one-year differences and the 6 (0.8%) other disagreements were two-year differences.

There was only 45% agreement in age determinations by scales and

otoliths (Table 3). Chi-square analysis (Table 4) indicated that age frequencies and the method of ageing were not independent ($P < 0.002$). Of the 363 disagreements between scale and otolith ages, 302 (83%) were one-year discrepancies, 55 (15%) disagreed by two years, and six (2%) disagreed by three years. Table 4 data show a greater frequency of ages 4 and 5 when otoliths are used for ageing, while there are more older representatives by scale analysis. The two opposing trends result in near identical estimates of the overall mean age, 5.96 (otoliths) and 6.05 (scales). Age six was estimated as the modal age by both methods of ageing.

Observed Age-Length Relationships

Mean observed fork length-at-age of adult females was consistently greater than that of males (Table 5). Overall, female fork lengths averaged 248 mm and males 238 mm; the difference was significant ($P < 0.0001$) (Fig 5).

F-tests showed a significant difference ($P < 0.01$) between variances of observed lengths-at-age from otoliths and lengths-at-age from scales of male alewives for all ages tested, but the direction of difference was not consistent. In contrast, the same analysis of data for female alewives showed no significant differences ($P > 0.05$) between the variances for the ages tested. For this reason, an approximation of the t-statistic (t') was used for comparing mean observed lengths-at-age by ageing methods for males, but for females the regular t was computed. There was no significant differences in mean lengths-at-age by methods ($P > 0.05$) for all of the ages tested (Table 5).

Relationship of Fork Length and Otolith/Scale Radius

Visual inspection of the plots of fork length on otolith radius for male and female alewives and the respective coefficients of determination ($r^2 = 0.78$ for males, $r^2 = 0.83$ for females) indicated that assumptions of linearity were reasonable. Furthermore, analysis of covariance indicated no significant difference ($P > 0.10$) in the two linear expressions. Thus, the relationship for the pooled data was:

$$L = -48 + 186.5 R_o; \quad (r^2 = 0.80)$$

where L = fork length and R_o = otolith radius.

Similarly, the relationships between fork length and scale radius were considered linear for males and females ($r^2 = 0.90$ and 0.88 , respectively). Analysis of covariance indicated a significant difference ($P < 0.01$) between the expressions; therefore, the data were not pooled and the relationship for males was:

$$L = 26 + 0.80 R_s$$

and for females:

$$L = 29 + 0.80 R_s$$

where R_s = scale radius.

Back-Calculated Lengths

Back-calculated lengths-at-age by sex (Tables 6, 7, 8, and 9) were less than mean observed lengths-at-age except for age 7 males. In general, back-calculated lengths for a given age were inversely related to age at capture, which indicates that positive "Lee's phenomenon" was present in the data (Ricker 1969).

Comparison of the Walford (1946) lines of males and females derived from lengths back-calculated from otoliths had significantly

different adjusted means ($P < 0.01$), but the two regression lines derived from scales were not significantly different ($P > 0.10$). As a result, sexes were not pooled in order that the Walford lines (Fig. 6 and 7) derived from the two ageing methods could be statistically compared. Analysis of covariance of the Walford lines from the two ageing methods was significant for females ($P < 0.001$), and marginally significant for males ($0.04 < P < 0.05$). Because of these differences between sexes and methods of ageing, data were not pooled for growth function determinations.

Growth Functions

Estimates of the von Bertalanffy growth parameters L_{∞} and t_0 were greater and K less for females than for males with both ageing methods (Table 10). Estimates of L_{∞} were greater and estimates of K and t_0 less when lengths-at-age were calculated from scales compared to calculations from otoliths. Since younger fish (males \leq age 4 and females \leq age 3) were estimated to be larger at a given age by otolith analysis than with scales, the growth curves cross at approximately age 7 for males (Fig. 8), and for females at age 4.8 (Fig. 9).

The weight-fork length relationships were significantly different for sexes ($P < 0.01$). The relationships were:

$$W = 3 \times 10^{-5} L^{2.83}; \quad (r^2 = .95)$$

$$\text{and } W = 1.6 \times 10^{-5} L^{2.94}; \quad (r^2 = .95)$$

for males and females respectively, where W = body weight without gonads, and L = fork length.

For the linear regressions of total length (TL) on fork length (FL) by sex, the regression coefficients were identical; however, the

adjusted mean lengths were significantly different ($P < 0.01$). This was as expected since females were larger than males at all ages. The respective equations for males and females for the fork length range of 83 to 300 mm were:

$$TL = 0.7 + 1.1 FL; \quad (r^2 = .99)$$

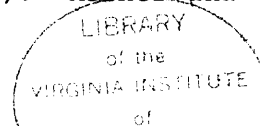
$$\text{and } TL = 1.4 + 1.1 FL; \quad (r^2 = .99).$$

DISCUSSION AND CONCLUSIONS

Age Determinations

Validation of otolith annulus formation will facilitate future VIMS monitoring of the alewife population in Virginia. The present findings indicate several advantages in using otoliths rather than scales for age and growth determinations of alewives. With a little experience the amount of time to remove and prepare otoliths for reading was considerably less than that needed to mount and press scales. Scales often required more reading time than otoliths because of the presence of false annuli and erosion. There was also a conservation of experimental units because of the low percentage of otolith discards (all but one pair were readable) in contrast to scales (32% discarded). Since alewives which were obviously damaged were culled at the time of sampling, the percentage of scales discarded in this study was probably minimized.

Another advantage of otoliths was the greater agreement between readers for otolith ages (83%) than for scale ages (77%). Mosher and



Eckles (1954) had 95% agreement of Pacific sardine ages from otoliths, but they only simulated two readers by having the same person read the otolith a day or more apart.

Agreement between otolith and scale age determinations was poor (45%) relative to the findings of some other investigators: 57% for alewife and 68% for blueback herring (Kornegay 1978); 81% and 62% agreement for haddock (Kohler et al. 1958); 68% agreement for Pacific sardine (Mosher and Eckles 1954); 68% for Atlantic herring (Messieh and Tibbo 1970); 86% for red porgy (Manooch and Huntsman 1977); and 75% for vermillion snapper (Grimes 1978). The low percentage of agreement in this study may be due to damaged scales in spite of the precaution of culling.

As in the present study where alewife age structure determined from otoliths tended to be younger than that determined from scales, Messieh and Tibbo (1970) had similar results with Atlantic herring. Kornegay (1978) reported no difference in alewife age frequencies by the two methods, but blueback herring otoliths gave a higher frequency for ages ≤ 5 than did scales. Possible explanations when age structure is younger from otolith analysis than from scales are that false annuli on scales have been interpreted as true annuli or the number of otolith annuli has been consistently underestimated due to the crowding of annuli at the otolith margin in older fish. In contrast, other investigators reported that age structure from otoliths were older than that from scales (Mosher and Eckles 1954; Kohler et al. 1958; Manooch and Huntsman 1977). Otolith analysis will give an older age structure than scales if excessive scale erosion deletes annuli or the number of annuli at the otolith margin is consistently overestimated. In

addition, the initial annulus formed on a scale is often hard to find and if frequently missed the frequency of younger ages will be underestimated.

Alewife scales, unlike internal otoliths, are prone to abrasion from contact with the substrate and other fish during the spawning migration through shallow water and during the act of spawning; therefore, duration on the spawning ground could affect the degree of scale damage. Kissil (1974) observed that alewives remained on the spawning grounds from 3 to 82 days. Cooper (1961) found that earlier migrating alewives remained on the spawning ground longer than fish in the later part of the spawning run. Loesch and Lund (1977) reported similar migratory and spawning behavior for the closely related blueback herring, Alosa aestivalis.

Observed Age-Length Relationships

On the whole, alewife observed fork lengths-at-age from scales were less than those reported by other workers in different areas: the Chowan River (Holland and Yelverton 1973); Albemarle Sound (Kornegay 1978); and lower Chesapeake Bay (Joseph and Davis 1965). Observed lengths-at-age from otoliths of Albemarle Sound alewives (Kornegay 1978) were also higher at a given age than those in this study.

In the present study and in Kornegay's (1978) observed fork lengths-at-age by the two methods of ageing were similar. The differences in observed lengths-at-age between the two studies indicated that ageing methodologies may have differed, or that there are differences in the growth rate of alewives in the Albemarle Sound and Chesapeake Bay areas.

Relationship of Fork Length and Otolith/Scale Radius

An advantage of using otoliths from Rappahannock River alewives for back-calculating growth was that the otolith radius on fork length regressions by sex could be pooled, but sexes had to be treated separately for the regressions of scale radius on fork length. The linear relationship between fork length and scale radius was consistent with the findings of other workers (Marcy 1969; Messieh 1977; Kornegay 1978); however, the linear relationship between fork length and otolith radius was not consistent with Kornegay (1978) who used a log fork length, and log otolith radius transformation to obtain linearity in his data.

Back-Calculated Lengths

The significant difference between sexes for the Walford lines based on otolith back-calculations of length-at-age is compatible with previous findings which show that female alewives are larger than males at a given age (Netzel and Stanek 1966; Marcy 1969; Holland and Yelverton 1973; Messieh 1977). In contrast, the non-significance between sexes for Walford lines derived from scale back-calculations is contrary to existing evidence. Back-calculated lengths-at-age were less than those computed by Kornegay (1978) from scales and otoliths of North Carolina alewives.

Growth Functions

Because L_{∞} and K are inversely related (Ricker 1975), the effect of these parameters on the shape of the growth curve was that growth

increments decay slower and asymptotic length is greater on the curves computed from scale age analysis than on the curves computed from otolith analysis. Messieh (1977) computed von Bertalanffy growth curves for alewives from scale back-calculations, but he found there were differences in the curves from different areas within the same river system.

The von Bertalanffy equations presented in this study will enable researchers to monitor changes in growth rates and associated parameters within the same area and compare it to growth curves in different areas. These equations are also useful for incorporation into Beverton and Holt yield-per-recruit analysis.

The total length-fork length relationships were presented so that data from this study can be readily transformed for comparison with other research in which total length is used.

General Comments

It is concluded, because of the ease of preparation, conservation of materials and closer reader agreement that the use of otoliths for age and growth determinations of alewives taken in the Virginia pound net fishery is superior to the use of scales. This difference in precision may not be inherent in scales and otoliths but a function of the fishery. Scale sampling should not be totally excluded because of the information scales contain on spawning history. The differences in the ageing methods may not be as great as in this study if samples are obtained from sources other than the commercial fishery, in which specimen damage is considerably less.

Table 1. Comparison of the number of disagreements within ageing methods between two workers for adult alewives.

	<u>Scale Readings</u>				
No. of years disagreement	<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>Total</u>
frequency	540	154	6	0	700
% of total	77	22	1	0	

	<u>Otolith Readings</u>				
No. of years disagreement	<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>Total</u>
frequency	596	113	10	1	720
% of total	83	16	1	0.1	

Table 2. Chi-square (X^2) test of independence between the number of agreements and disagreements and the methods of ageing.

	<u>Agree</u>	<u>Disagree</u>	<u>Total</u>
Scales	540	160	700
Otoliths	596	124	720
Total	1136	284	1420

$X^2 = 7.04$ with 1 degree of freedom ($P < 0.01$)

Table 3. Comparison of individual age determinations from scales and otoliths of Rappahannock River alewives.

<u>Otolith Age</u>	<u>Scale Age</u>						<u>Total</u>
	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	
4	1	3	4	0	0	0	8
5	3	73	101	29	3	0	209
6	0	55	193	65	4	0	317
7	0	10	59	24	10	2	105
8	0	1	5	5	1	1	13
9	0	0	1	1	0	0	2
<u>Total</u>	4	142	363	124	18	3	654

Table 4. Chi-square (χ^2) test of independence between age frequencies and the methods of ageing.

	<u>Age</u>						<u>Total</u>
	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	
<u>Otoliths</u>	8	209	317	105	13	2	654
<u>Scales</u>	4	142	363	124	18	3	654
<u>Total</u>	12	351	650	229	31	5	1308

$\chi^2 = 19.82$ with 5 degrees of freedom ($P < 0.002$)

Table 5. Observed mean fork lengths (FL), standard error (SE), and t-statistic for male (M) and female (F) Rappahannock River alewives.

	Age	No.		FL		SE		t	
		M	F	M	F	M	F	M	F
Otolith	4	5	2	221	221				
Scale		3	1	229	185				
Otolith	5	137	76	236	242	0.86	1.13	0.90 ^{1/}	1.53
Scale		112	71	237	245	0.70	1.13		
Otolith	6	193	145	240	248	0.64	0.79	1.28 ^{1/}	0.69
Scale		217	145	238	248	1.20	0.75		
Otolith	7	45	50	242	254	1.39	1.22	1.01 ^{1/}	1.94
Scale		58	58	240	251	1.70	1.15		
Otolith	8	2	11	241	257				3.16
Scale		2	4	258	259				
Otolith	9	1	1	242	261				
Scale		0	1		268				

^{1/} Approximation of t (t') due to unequal variances.

Table 6. Back-calculated fork lengths-at-age from otoliths of male Rappahannock River alewives.

Back-calculated fork lengths (mm) of successive ages

Age at Capture	#	1	2	3	4	5	6	7	8	9
4	5	120	166	198	221					
5	139	110	157	193	215	236				
6	191	107	152	186	207	224	240			
7	45	101	147	179	199	217	229	242		
8	2	98	139	179	204	219	228	234	241	
9	1	95	140	177	191	204	215	225	232	242
Weighted Means		107	154	187	209	227	238	241	238	242

Table 7. Back-calculated fork lengths-at-age from otoliths of female Rappahannock River alewives.

Back-calculated fork lengths (mm) of successive ages

Age at Capture	#	1	2	3	4	5	6	7	8	9
4	1	153	166	213	252					
5	76	114	160	194	219	242				
6	145	110	156	190	213	231	248			
7	50	104	151	187	210	228	241	254		
8	11	95	145	180	207	224	237	247	257	
9	1	115	143	178	205	212	230	251	254	261
Weighted Means		110	156	190	214	233	245	253	257	261

Table 8. Back-calculated fork lengths-at-age from scales of male Rappahannock River alewives.

Back-calculated fork lengths (mm) at successive ages

Age at Capture	#	1	2	3	4	5	6	7	8
4	3	130	181	205	229				
5	112	102	146	190	216	237			
6	217	99	140	181	206	226	237		
7	58	95	134	169	195	216	231	240	
8	2	104	152	188	215	229	246	251	258
Weighted Means		99	141	182	208	228	236	240	258

Table 9. Back-calculated fork lengths-at-age from scales of female Rappahannock River alewives.

Back-calculated fork lengths (mm) at successive ages

Age at Capture	#	1	2	3	4	5	6	7	8	9
4	1	72	145	170	185					
5	71	106	157	197	222	248				
6	145	104	148	189	215	236	246			
7	58	99	137	177	204	226	241	243		
8	4	102	153	184	215	235	247	255	259	
9	1	103	142	162	190	220	244	257	263	268
Weighted Means		103	148	188	214	237	245	244	260	268

Table 10. Von Bertalanffy growth parameters calculated from scale and otolith back-calculations.

	\underline{L}_{∞}	\underline{K}	\underline{t}_0
<u>Scales</u>			
Males	264	.3395	.3847
Females	282	.3128	.4340
<u>Otoliths</u>			
Males	257	.3814	.4091
Females	272	.3367	.5560

Fig. 1. Scale of an age five Rappahannock River alewife.



Fig. 2. Otolith of an age five Rappahannock River alewife.



Fig. 3. Otolith of a young-of-the-year alewife caught in August in the Rappahannock River.



Fig. 4. Otolith of an age one alewife caught in February off the mouth of Chesapeake Bay.



Fig. 5. Length-frequencies of male and female adult Rappahannock River alewives.

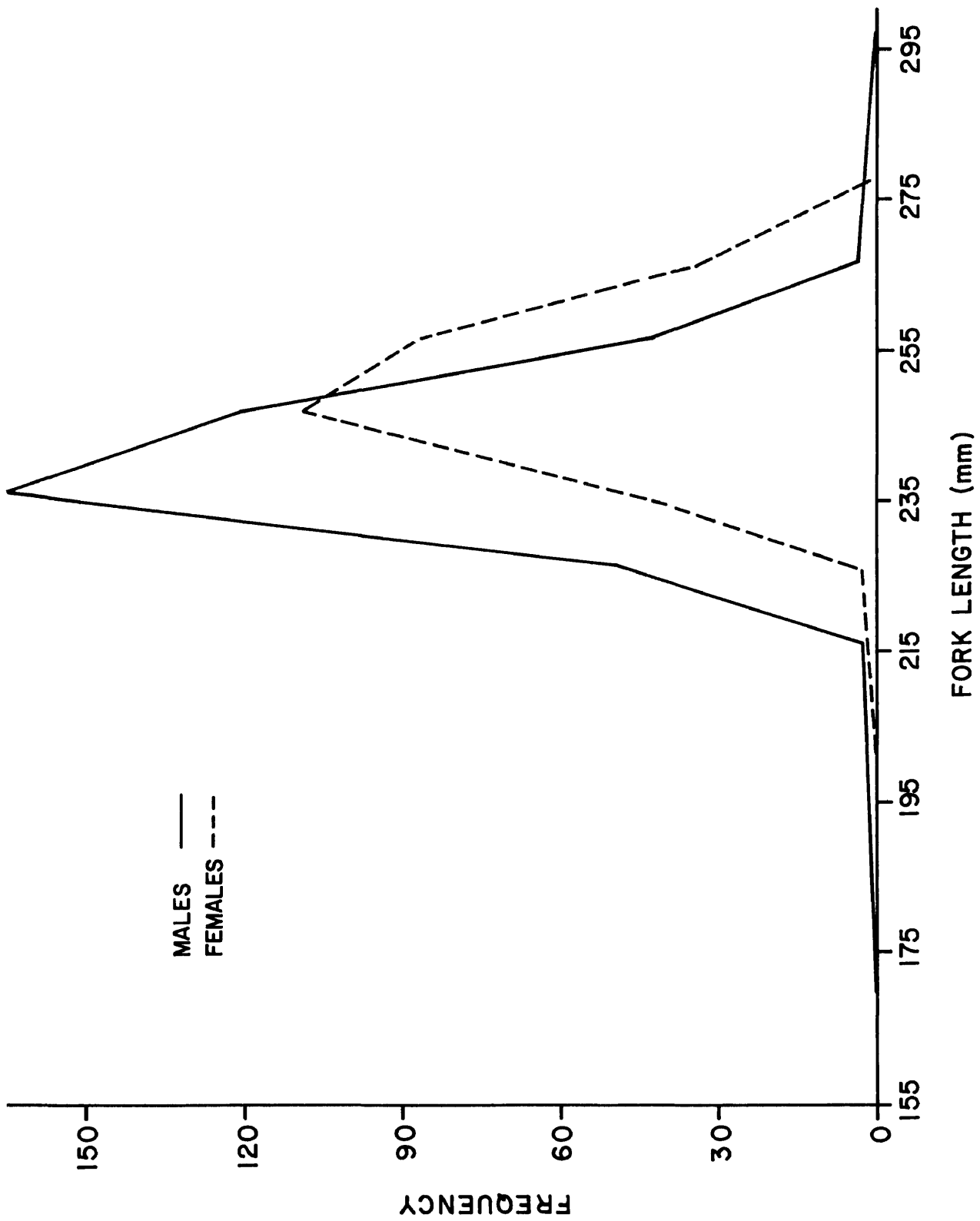


Fig. 6. Walford regression of length (mm) at age $t+1$ on length (mm) at age t derived from otoliths.

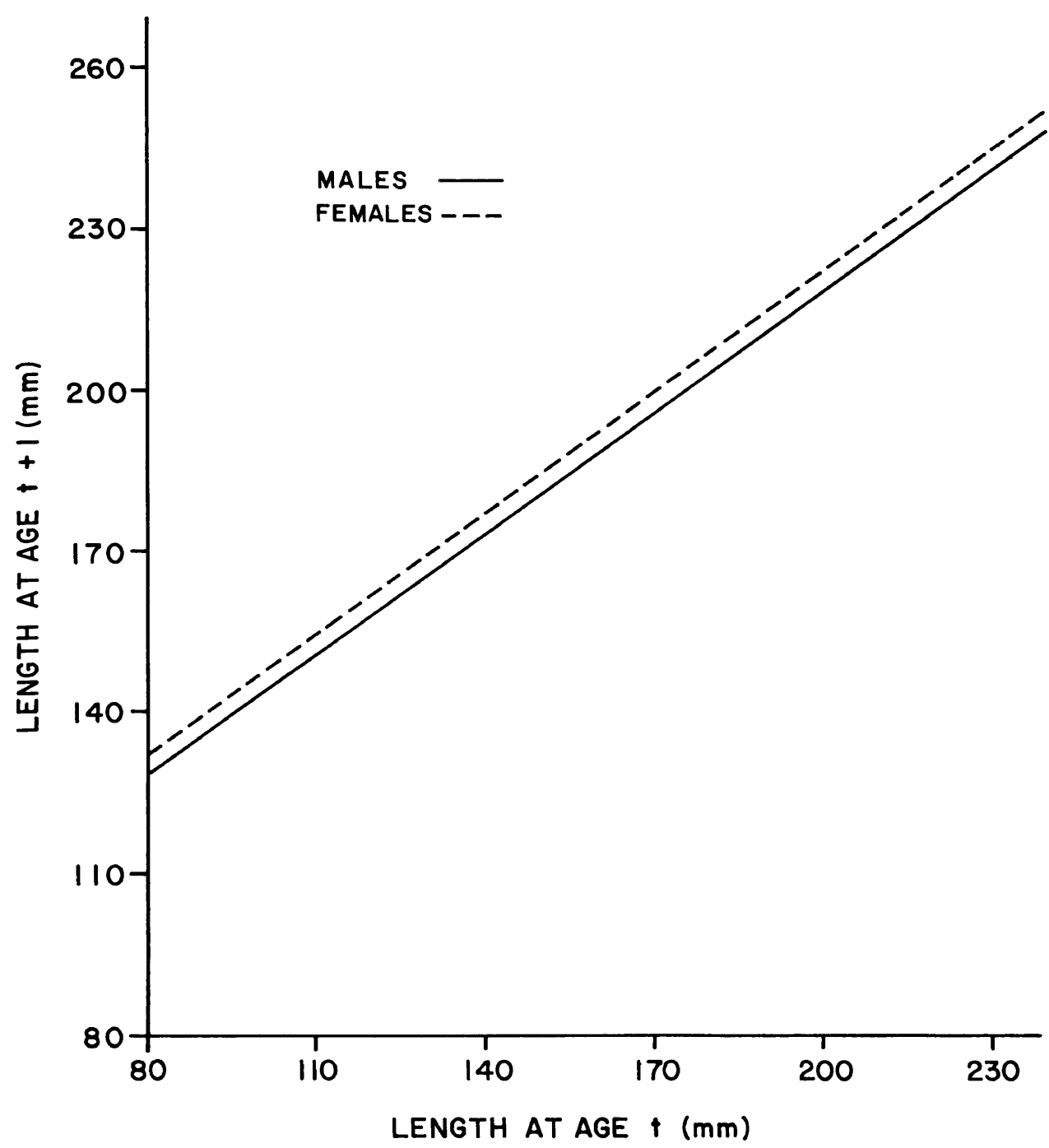


Fig. 7. Walford regression of length (mm) at age $t+1$ on length (mm) at age t derived from scales.

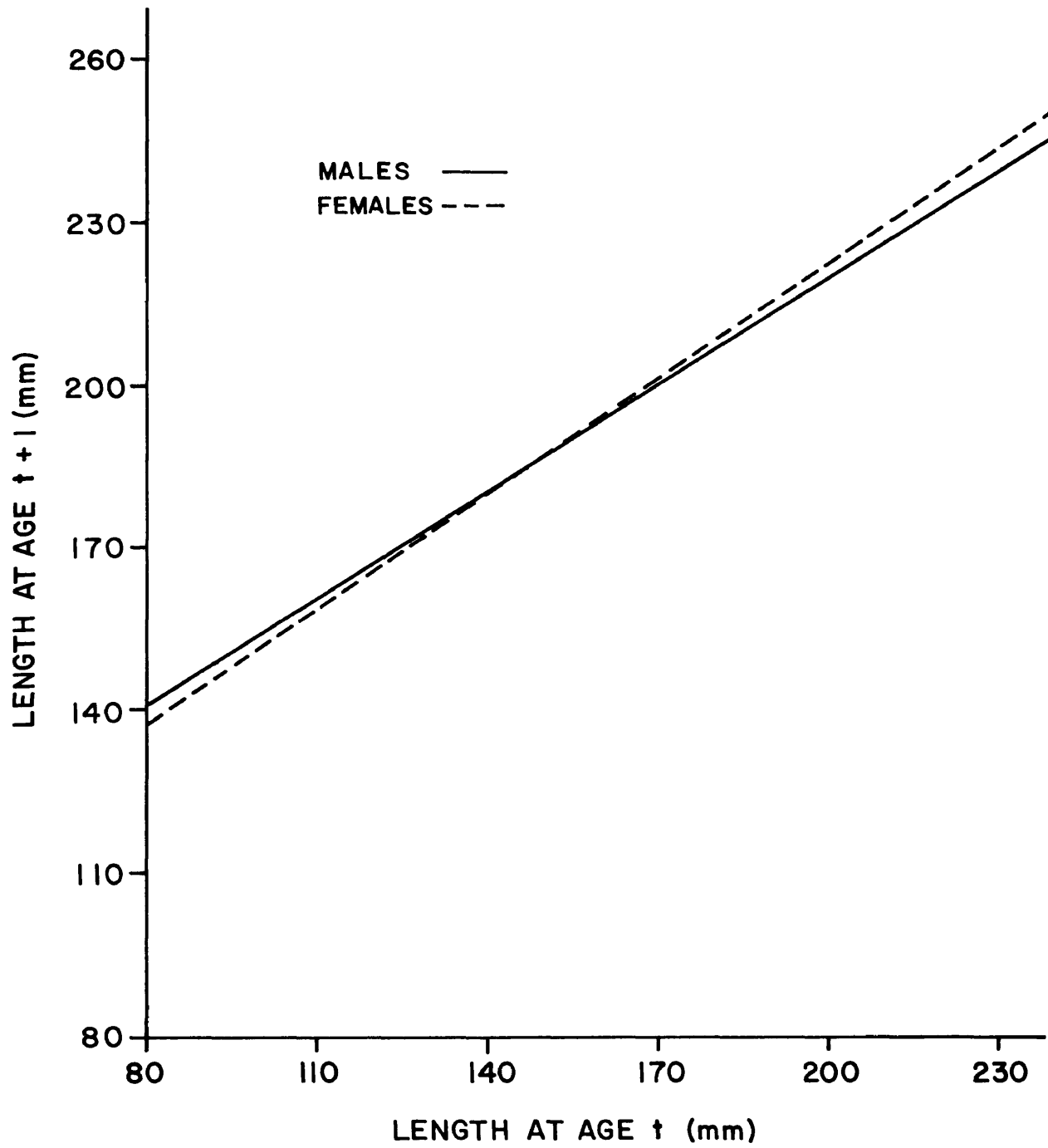


Fig. 8. Von Bertalanffy growth curves of male alewives from scale and otolith back-calculations.

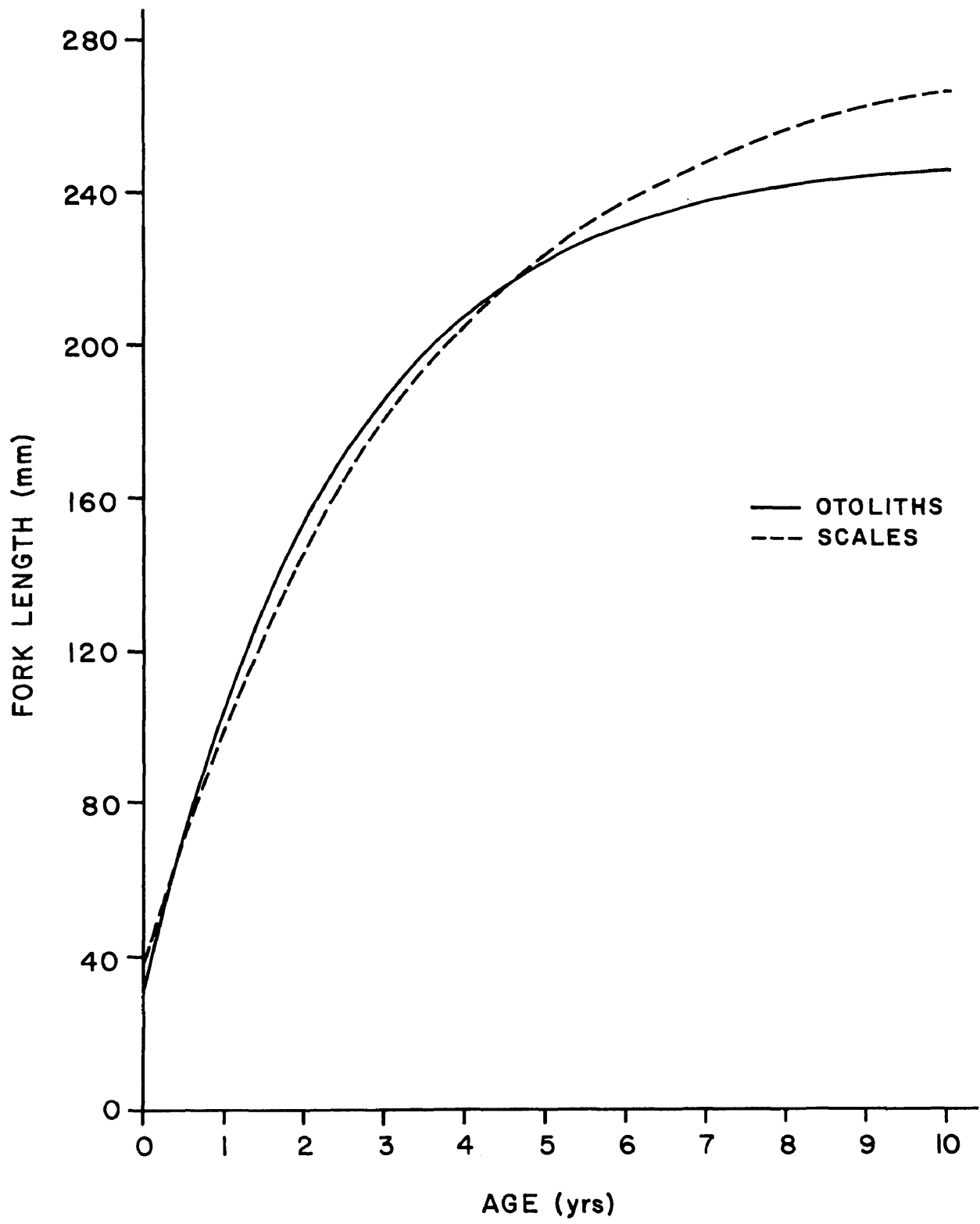
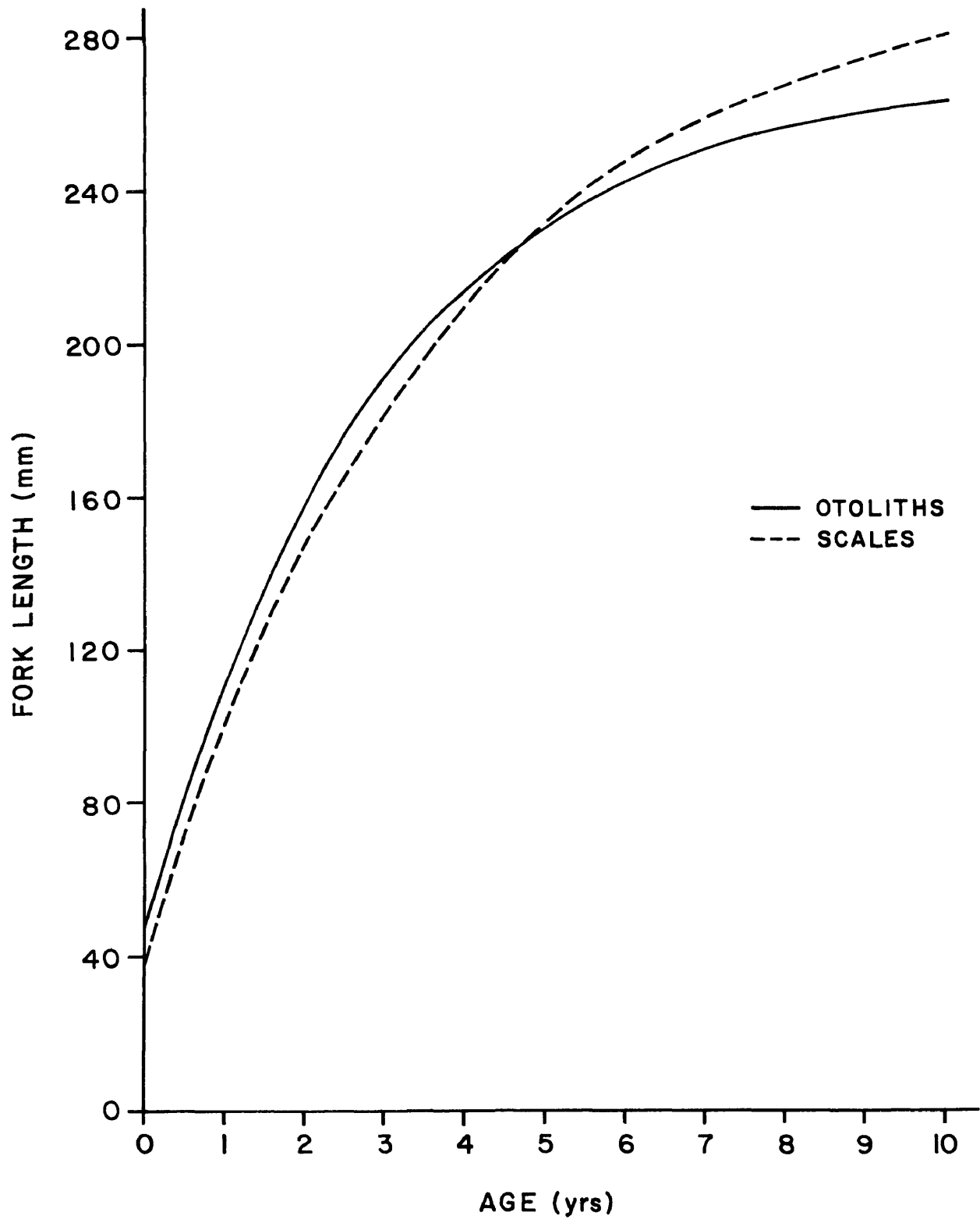


Fig. 9. Von Bertalanffy growth curves of female alewives from scale and otolith back-calculations.



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