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Age Determination and Growth of Tiger Flathead

(*Platycephalus richardsoni*)

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Running head: Age determination and growth of tiger flathead.

Abstract

This study revises the methodology used to determine the age and growth of tiger flathead (*Platycephalus richardsoni*) in south-east Australian waters.

Tiger flathead were sampled monthly from commercial landings and research survey vessel catches over the 24-month period commencing January 1983. Counts of the number of 'true' annuli in the saggital otoliths were used for age determination. It is shown that (i) a hyaline annulus is laid down each spring period, (ii) the effects of masking of the inner annuli due to thickening in the central part of the otolith can be systematically corrected for, (iii) 'supernumerary' annuli can be identified, their non-periodic nature demonstrated and annular counts corrected for 'true' periodic annuli, and (iv) once corrected, annuli are consistent and unbiased estimators of age across all age classes.

The von Bertalanffy growth parameters are estimated. Male (K = 0.178, L_{oo} = 48.150 cm) and female (K = 0.159, L_{oo} = 58.78 cm) growth rates are statistically different, females growing to a larger length at age. It is

shown that previous studies underestimate longevity and overestimate growth rate by a factor of about two.

Introduction

The tiger flathead (*Platycephalus richardsoni*) is a species of major economic importance to the south-east Australian trawl fishery. Since the inception of the fishery in 1915 to the immediate post-Second World War period this fishery was based almost entirely on this species, which represented approximately 90% of total landings (Fairbridge 1952). Landings increased to about 5,000 t and then declined due to a collapse in catch rates to less than 2,000 t by the early 1980's (Anon. 1985). Even at the present level of landed catch the tiger flathead resource represents a major source of fresh fish to the populous south-east of Australia, although its economic importance has declined.

Present trends indicate that this decline in landed catch may be reversing, with substantial increases in landings reported from the southern part of the range of the species, east of Bass Strait. This raises the problem of potential over-exploitation of the resource since it appears that the population has historically been unable to sustain landings of 5,000 t. Estimated standing stock in the southern half of the range (Wankowski 1984, Wilson 1984), although likely underestimates, support this view.

The most common method of rationally managing a fishery resource requires estimation of sustainable (or some other) yield or a fishing mortality parameter, and a variety of models are available for this purpose (e.g. Schaefer and Beverton 1963, Deriso 1980, Pope and Shepherd 1982). These models require estimates of population (or catch) structure by age class and/or an estimate of the parameters of a growth function for which a relatively accurate and verifiable age determination procedure is necessary.

Tiger flathead age determination has been undertaken by several studies using the convential technique for temperate fish species, counting the number of growth discontinuities, that is annuli, observable in the structure of the sagittal otoliths. In order to successfully determine the age of fish from otoliths it is necessary to detect periodic annuli, determine the timing and periodicity (annual or other) of annulus formation, and correct annular counts for obscuring by increased thickening with age and the presence of non-periodic (or extra-periodic) supernumerary annuli where these occur.

This procedure was first applied to tiger flathead by Dakin (1939) who described the annular structure of the otolith in this species and determined five 'year groups' in fish between 15 and 45 cm total length (TL). Dakin was unable to verify the periodic nature of the annuli nor the timing of annulus formation, and inferred an annual periodicity from the life history of the species. Furthermore only a small proportion of otoliths were found to be suitable for age determination. Irregularly spaced annuli, 'false' annuli and obliteration of one or more annuli were reported to be a very common feature.

Fairbridge (1951) provided a very detailed description of the tiger flathead otolith and confirmed the existence of Dakin's (op. cit.) five 'year groups', although mean lengths at age were very slightly different. His results showed that in I and II group fish the annulus formed in May, but in older fish the timing of annulus formation was unclear. Fairbridge's general conclusion was that tiger flathead otoliths were 'not good' for age determination, and found that supernumerary annuli and obliterated first annuli were a major problem in all age groups. However, he was able to verify the age for group I and II fish from length frequency modal progressions, but this was not possible for older age groups. For older fish an additional problem was an increase in transluscent areas (i.e. hyaline zones normally found between the opaque annuli). As a consequence of the interaction between increase in the occurrence of apparently supernumerary annuli and increased extent of hyaline zones, he reports that in fish of group III and older (33.1 cm TL) selection of 'true' annuli was frequently based on the expected length of fish for a particular annulus count.

Houston (1955) claimed that Fairbridge (op. cit.) underestimated age groups by one year, but no supporting evidence was provided. Finally, Montgomery (1983) in an unpublished manuscript presented a recent review of tiger flathead growth and determined ages at length that were roughly equivalent to Fairbridg's (op. cit.) plus one year (i.e. similar to Houston's interpretation). Ages to group VIII, approximately 51.4 cm fork length (FL), were reported.

The present study was initiated for several reasons. It was primarily motivated by attempts to model the population dynamics of the eastern Bass Strait stock, the outcome of which were estimates of stock net turnover rates and other population parameters inconsistent with fishery dynamics and the life history of the species. Inaccuracy in otolith measurements using conventional methods was high and the selection of 'good' otoliths appeared to be resulting in errors in age estimation. The major problems were:

1. Using the established age at length relationship the survival rate between age classes (calculated from age composition data from commercial landings and independent research vessel samples) was between 10% and 25%. This is neither consistent with the relatively low fishery-induced mortality rate (Wankowski and Hobday 1984, Anon. 1985) nor, in the absence of a very high fishery-induced mortality, the biology of the species.

2. As noted by previous authors, tiger flathead otoliths (although better than other hard parts or scales) exhibit great variability.

3. This is compounded by otolith measurement inaccuracies when conventional microscope and eyepiece graticule methods are used.

4. Examination of a range of otoliths confirmed earlier observations that the central part tended to be obscured in larger fish, masking early annuli.

5. The selection criteria used to distinguish 'supernumerary' annuli in larger fish were subjective and had not been subject to verification.

6. A proportion of otoliths from very large fish were unclear and therefore rejected. Furthermore about 50% of otoliths in which annuli were clearly discernable suffered from masking of the central part of the otolith and about 20% exhibited other irregularities of the central part. It is necessary to demonstrate equivalence in growth between these groups before estimating a growth function representative of the whole population, since it is possible that a growth function based on a selective sub-sample of less than 30% of the population might not be representative of that population as a whole.

In this paper we demonstrate that the periodicity of 'true' annuli is annual and that these are a consistent and unbiased estimator of age for all age classes. We derive the parameters of the von Bertalanffy (Bertalanffy 1960) growth function and demonstrate that previous studies overestimate growth rate and underestimate longevity. This has obvious implications with regard to the understanding of population dynamics and management of the fishery. A methodology was also developed to reduce variation between individual otolith data due to measurement errors and inaccuracies and operator bias due to age at length expectations.

Methods

Monthly length-stratified (by 1.0 cm FL class) randomised samples of fish were taken from the commercial landings and from research survey catches from the eastern Bass Strait area over the 24-month period commencing January 1983. In total 1613 fish were sampled. The sample comprised two parts, (i) a 12-month sample (commencing January 1983) which comprised the widest-possible size range of fish (12.3 to 58.4 cm FL), and (ii) a smaller second year's sample of intermediate-length fish. Fish FL was measured to the nearest mm.

The sagittal otoliths were removed through the roof of the buccal cavity and dried at room temperature for at least two months prior to examination. A full description of the sampling regime and treatment are provided in Moulton and Wankowski (1985a, b).

Examination was accomplished immediately following immersion of each pair of dry otoliths in water. Various techniques have been used to improve clarity and resolution, including, for tiger flathead, grinding (Dakin 1939), immersion in clearing agents (Fairbridge 1951) and immersion in water for 12 hours (Montgomery 1983). We found that none of these techniques improved clarity to any significant degree, and clearing or prolonged immersion in water often resulted in increased transluscency to the detriment of contrast between the hyaline and opaque bands near the margin of the otolith. This last effect may result in the 'loss' of marginal annuli.

The otoliths of tiger flathead are elongated, slightly curved and with relatively smooth margins, with a small anterior rostrum (Fig. 1). Annuli are clearly seen against a dark background as bands of hyaline material alternating with opaque. The otoliths exhibit great variability between individuals. Irregularly spaced non-periodic 'supernumerary' annuli are frequently present, and these are visually distinguished on the basis of being incomplete, of reduced width and irregular occurence between the thicker, complete periodic annuli. A large number of otoliths show an opaque, thickened centre. A proportion of individuals also exhibit other irregularities in the central part of the otolith.

That the 'supernumerary' annuli are indeed non-periodic and fall outside the regular pattern of growth was clear when attempting to validate that annulus increments were consistent between ages as described in a subsequent part of this paper. The results were consistent only when 'supernumerary' annuli were excluded.

Measurements from each otolith were taken using a 28 x 28 cm working area digitising pad (Summagraphics bitpad) and LED cursor linked to a microcomputer (Apple 11e), and using appropriate software. A dissecting microscope and drawing tube were used to superimpose the otolith image over the working area of the pad. The co-ordinates of the otolith centre, the inner edge of each hyaline band and the otolith margin along the axis from the centre to the posterior edge of the otolith were recorded. Since co-ordinates only are recorded, and not measurements, the potential impact of operator expectations with regard to annulus radii is minimised. The otolith radius, the radius of each annulus and the marginal increment (the distance from the outermost annulus co-ordinate to the edge of the otolith) were calculated and used for validation purposes. The age of each fish was determined from the number of complete periodic annuli, so that an otolith with i complete hyaline bands plus an opaque margin was designated as age class i.

The percent of expected marginal increment (% EMI, Davis 1977) was calculated and standardised from the full 24-month sample:

$$\% \text{ EMI} \cdot \frac{E(R_N)}{R_n}$$

where: $$\% \text{ EMI} = \frac{R_n - R_{ni}}{E(R_{(i+1)} - R_i)} \cdot 100$$

R_n is the measured radius of otolith n.

R_{ni} is the measured radius of the outermost complete annulus (annulus i) of otolith n.

$E(R_{(i+1)} - R_i)$ is the expected increment between annulus i and annulus i + 1.

$E(R_n)$ is the expected radius of otolith n.

$E(R_n)$ was calculated by interpolation on the regression of otolith radius on fish FL. The full 24-month sample was used.

Growth in length was estimated by the von Bertalanffy growth function (Bertalanffy 1960) using the BMDP monlinear estimation package (BMDP Statistical Software Inc., Los Angeles, USA). Data from the first 12 months of the study were used in the estimation.

The von Bertalanffy function may be written:

$$L_t = L_{oo} (1 - \exp(-K(t - t_o)))$$

where: L_t is the fork length at age t

L_{oo} is asymptotic length

K is a parameter describing how rapidly L_{oo} is achieved

t_o is the hypothetical age at length zero.

The "extra sum of squares principle" (Draper and Smith 1979) F-test was used to compare growth between sexes. Since a proportion of the sample comprised immature fish, and since these contributed to contrast in the sample, these were included in both male and female regressions. However, since the F-test requires independent samples, immature fish were not included in the test data. Joint confidence regions for the parameters of the von Bertalanffy function were plotted using the method of Kimura (1980).

Results

Annulus consistency between age classes

For valid and repeatable age determination it is essential that the age of each individual is determined using annuli in the same relative position. That is, that the i th annulus in individual n is in the same position as the i th annulus in individual n + 1. This pre-supposes that otolith growth is consistent between individuals and proportional to growth of the whole animal. In well-behaved material annulus consistency is normally assumed, but in this case it is necessary to demonstrate this. Therefore, in this section we show that the effects of masking due to thickening in the central part of the otolith can be systematically corrected for, and that once corrected inter-annular increments and therefore relative annulus position are consistent and unbiased across age classes.

Otoliths were divided into three groups:

1. Those with an opaque central zone.
2. Those with a thickened and occluded central area which clearly extended beyond the inner opaque zone.
3. Those with other irregularities in the central area.

Approximately 20% of the total pairs of otoliths fell into group three. In this group it was impossible to distinguish 'true' annuli from other annuli except by excluding those annuli where inter-annular increments did not fit the pattern established from the other 80% of the sample. These were therefore excluded since if the 'true' annuli were selected in this way they would add nothing to the analysis.

The distribution of annulus radius by group for groups one and two for the innermost two annuli clearly show that the two groups belong to seperate statistical populations (Tables 1 and 2). For males, the mean distance (+/- two standard deviations) from the otolith centre of the first (innermost) annulus for group one is 1.71 mm (0.89 - 2.53) and that for group two is 3.17 mm (2.89 - 3.45), which is almost identical to the mean radius for the second annulus for group one (3.27 mm, 1.87 - 4.67). The second annulus for group two also clearly belongs to a different distribution from the second annulus of group one. A similar situation holds for the females. The pattern remains clear for later annuli.

The 'loss' of one annulus in group two fish implies that annular counts for this group underestimate age class by one. It is therefore expected that the mean length at age j for group one would be equal to mean length at age j - 1 for group two. This is confirmed by the data (Table 3) where this correspondence is almost exact.

There were no consistent or periodic annuli found in any otoliths closer to the otolith centre than the innermost annulus of group one fish. This annulus position is the baseline position from which counts and inter-annular increments are taken. The data on annulus counts and measurements for group two fish used in the remainder of this paper have been corrected so that the innermost annulus of group two fish is equivalent to the second annulus of group one fish. That is, in the combined (groups one and two) data set, data on annular counts, radii and inter-annular increments for the i th annulus are made up of the i th annulus for group one fish and the (i + 1) th annulus for group two fish.

Regressions of inter-annular increment on annular count for the combined data set (Table 4) demonstrate that the periodic or 'true' annuli identified in this study are a consistent feature over all age classes. The slope of each regression was not statistically different from zero ($P < 0.01$) in all but two cases (excluding the first increment), indicating no trend in annulus increment with age of fish. The increment to the first annulus (0/1: from the otolith centre to the innermost annulus) showed a large variability. This is likely a consequence of variation in the time to first annulus formation due to the protracted spawning season (of about five months in the study area, from September/October through January/February (Wankowski, unpublished data)). This increment cannot therefore be considered an indicator of annulus consistency. No attempt has been made to assign a date of birth.

Validation of annual annulus periodicity

Regression of otolith radius on fork length for males and females (Table 5) were both significant at the $P < 0.0001$ level and confirm Fairbridge's (1951) finding.

The annual nature of 'true' annulus formation was confirmed by the distribution of the standardised %EMI with time (Fig. 2). It is clear that in the population as a whole annuli are laid down over a period of time in the autumn and winter between September and February, which corresponds with Fairbridge's (1951) finding for very young fish.

Growth

The von Bertalanffy parameters K, L_{oo} and t_o were estimated (Table 6, Fig. 3) using all data points. The F-test indicated a significant difference between the growth of males and females ($P < 0.005$, Table 7). The plot of 95% confidence regions around K and L_{oo} (Fig. 4) indicates overlap between estimates of K for the two sexes, but differing L_{oo} values. The implication is that rate of growth is comparable between the sexes, but females grow to a larger (maximum theoretical) body length.

Discussion

The tiger flathead belongs to that group of fish where date of birth and the timing of formation of an annual growth mark vary widely between individuals. The consequence of this is extreme variability between otoliths and therefore uncertainty in age estimation. Uncertainty also results in wide confidence intervals and therefore difficulties in demonstrating the statistical significance of the age validation procedure and the age-length relationship. In our opinion this can result in unacceptable errors.

In the present study we have reduced between-otolith variability by (i) reducing measurement errors using the digitising technique rather than eyepiece graticule or comparable methods, (ii) maximising the proportion of 'good' (that is useable) otoliths by systematically correcting for occlusion of annuli, and (iii) correcting for the variation in time of formation of the first annulus. Because of this it has also proved necessary to unequivocally demonstrate that the 'true' annuli used in age estimation are consistent between age classes.

The estimated ages at length from previous studies are compared with the present results by fitting the von Bertalanffy function to published data for the same area and comparing the results using an F-test (Draper and Smith, 1979). It is clear from the outcome (Fig. 5 and Table 8) that previous studies overestimate growth rate and underestimate longevity by a factor of approximately two. Dakin's (1939) data broadly agree with the present study only for age class 1. Fairbridge's (1951, Table 14, for the Tathra-Disaster Bay area which is latitudinally comparable to the present study area) age group II agree with our age class 3 (for females) and 4 (for males). Montgomery's (1983) results do not agree with the present study except for age classes 3 and 4 (for males) and 4 and 5 (for females). This is likely to be at least partly attributable to the absence of younger age classes in his data, and high (and positive) t_0 values (Fig. 5).

As discussed in the introduction, overestimation of growth rate can have serious consequences when estimating net turnover rates for the population. We suggest that since age determination is dependent on counting the number of annuli and that about 60% of 'useable' tiger flathead otoliths (i.e. groups one and two) have the first annulus occluded, use of all 'useable' otoliths to estimate a growth function will result overall in underestimation of age at length unless an appropriate correction is made. Furthermore, selection of 'true' vs 'supernumerary' annuli is critical to counts of annuli, in particular for older fish. We suggest that the annular radii shown in Table 9 are used as a guide in establishing 'true' annuli for this species.

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TABLE 1. Mean annulus radii (mm) for male tiger flathead. Group one (top) and group two (bottom). SD: standard deviation. Note that mean radius for annulus i group one is equivalent to mean radius for annulus i + 1 group two.

Age Class	Annulus number 1	2	3	4	5	6	7	8	9	10
2	1.93	3.86								
3	2.07	3.97	5.31							
4	1.16	2.35	3.95	4.56						
5	2.14	3.86	5.10	5.91	6.52					
6	1.93	3.49	4.84	5.73	6.37	6.81				
7	1.91	3.51	4.81	5.75	6.45	6.92	7.28			
8	1.90	3.36	4.66	5.54	6.22	6.83	7.38	7.71		
9	1.67	3.19	4.43	5.42	6.27	6.87	7.32	7.64	7.91	
10	1.53	2.61	3.95	4.77	5.74	6.45	7.05	7.43	7.74	8.04
Mean	1.71	3.27	4.60	5.14	6.39	6.83	7.29	7.63	7.87	8.04
SD	0.41	0.70	0.59	0.61	0.18	0.12	0.09	0.09	0.07	
2	3.22	4.78								
3	3.06	4.87	6.02							
4	3.16	4.84	5.77	6.41						
5	3.29	4.72	5.64	6.30	6.82					
6	3.20	4.68	5.58	6.19	6.75	7.16				
7	3.16	4.51	5.47	6.27	6.83	7.29	7.64			
8	2.65	3.77	4.66	5.70	6.29	6.74	7.12	7.51		
9	2.96	4.11	5.19	6.02	6.63	7.18	7.65	7.80	8.34	
Mean	3.17	4.69	5.63	6.26	6.75	7.12	7.48	7.74	8.34	
SD	0.14	0.25	0.27	0.16	0.14	0.15	0.25	0.25		

TABLE 2. Mean annulus radii (mm) for female tiger flathead. Group one (top) and group two (bottom). SD: standard deviaition. Note that the mean radius for annulus i group one is equivalent to mean radius for annulus i + 1 group two.

	Annulus number											
Age Class	1	2	3	4	5	6	7	8	9	10	11	12
2	1.90	3.94										
3	1.97	3.85	5.29									
4	2.07	4.15	5.51	6.61								
5	2.41	4.42	5.57	6.58	7.32							
6	2.35	4.01	5.28	6.21	6.97	7.63						
7	2.10	3.81	5.20	6.10	6.86	7.47	8.05					
8	1.90	3.48	5.00	6.09	6.99	7.73	8.29	8.70				
9	2.14	4.11	5.48	6.47	7.36	8.01	8.52	8.93	9.26			
10	1.78	3.18	4.47	5.52	6.41	7.23	7.82	8.33	8.74	9.07		
11	1.94	3.55	4.97	5.92	6.81	7.46	8.04	8.53	8.95	9.25	9.52	
12	1.49	3.24	4.65	5.70	6.58	7.31	7.88	8.36	8.77	9.11	9.37	9.54
Mean	2.07	3.88	5.21	6.20	6.95	7.56	8.09	8.56	8.90	9.13	9.45	9.54
SD	0.24	0.34	0.31	0.34	0.28	0.20	0.23	0.22	0.21	0.07	0.08	
2	3.39	5.40										
3	3.18	5.23	6.43									
4	3.45	5.36	6.48	7.28								
5	3.34	4.92	6.02	6.90	7.58							
6	3.16	4.79	5.89	6.73	7.46	8.01						
7	3.15	4.71	5.87	6.75	7.46	8.03	8.48					
8	3.27	4.97	6.16	7.06	7.73	8.26	8.67	8.99				
9	3.20	4.76	5.89	6.71	7.42	7.96	8.45	8.82	9.14			
10	3.23	4.86	5.91	6.69	7.46	8.09	8.60	9.02	9.37	9.61		
11	2.85	4.48	5.56	6.56	7.47	8.10	8.55	8.97	9.35	9.63	9.90	
Mean	3.25	4.92	6.02	6.86	7.53	8.06	8.54	8.95	9.25	9.62	9.90	
SD	0.11	0.21	0.20	0.18	0.09	0.09	0.09	0.09	0.12	0.01		

TABLE 3. Mean length at age for group one and group two fish. Note that mean length at age i for group one fish corresponds almost exactly to mean length at age i - 1 for group two.

Age Class	Mean length (FL, cm) at age			
	Males		Females	
	Group one	Group two	Group one	Group two
1				27.1
2	22.7	28.4	24.2	31.0
3	28.1	32.0	28.9	33.3
4	31.8	33.4	34.3	38.4
5	33.1	35.4	37.6	40.2
6	34.7	36.6	40.2	42.1
7	38.3	39.3	42.6	45.0
8	39.9	40.2	45.2	47.2
9	41.3	42.4	48.2	49.6
10	41.8		48.3	51.0
11		47.5	50.7	50.9
12	47.7		51.2	54.7
13			55.8	
14				

TABLE 4. Regression slope coefficient (b), standard error (SE) and the outcome of testing $H_0 : b = 0$ ($P < 0.01$) for regression of annular increment on age class for male (top) and female (bottom) tiger flathead. NS: slope coefficient not significant, i.e. accept H_0. Annular increment 0/1: radius of innermost annulus, 1/2: increment between annulus 1 and 2, 2/3: increment between annulus 2 and 3, and so on.

	0/1	1/2	2/3	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11	11/12	12/1
b	−0.092	−0.021	−0.045	0.002	0.010	0.022	0.022	0.013	0.015	0.015	−0.003	0.002	–
SE	0.02	0.030	0.014	0.008	0.009	0.005	0.008	0.007	0.007	0.008	0.007	0.003	–
		NS	NS	NS	NS		NS	NS	NS	NS	NS	NS	
b	−0.018	−0.031	−0.002	0.002	−0.003	0.005	0.004	0.011	−0.003	Insufficient			0.011
SE	0.016	0.014	0.018	0.003	0.008	0.005	0.005	0.002	0.005	data			0.005
	NS	NS	NS	NS	NS	NS	NS		NS				NS

TABLE 5. Linear regression of otolith radius (mm) on fish fork length (cm), for male and female tiger flathead. SE: standard error, both regressions were significant at the $P < 0.0001$ level.

	SLOPE	INTERCEPT	SE	R^2
Male	0.168	1.18	0.003	0.876
Female	0.167	1.19	0.002	0.898

TABLE 6. Estimated parameters of the von Bertalanffy (Bertalanffy 1960) growth function. L_{oo} in FL (cm), t_o in years, K on an annual basis, N: number in sample, asymptotic standard deviation of each parameter in parentheses.

Sex	K	L_{oo}	t_o	N
Males	0.1782	48.15	-1.687	557
	(0.0214)	(1.7049)	(0.3363)	
Females	0.1599	58.78	-1.220	677
	(0.0122)	(1.4219)	(0.2073)	

TABLE 7. Results of F-test comparing growth between male and female tiger flathead using mean length at age weighted by number in age class. RSS = residual sum of squares, d.f.: degrees of freedom. The test is significant at $P < 0.005$.

	RSS	d.f.
Male	373.7	10
Female	278.1	11
Combined	10281.8	25

$$F_{(4, 21)} = \frac{(10281.8 - (373.7 + 278.1))/(25-21)}{(373.7 + 278.1)/(10 + 11)} = 77.56$$

TABLE 8. Von-Bertalanffy parameters for Fairbridge's (1951, Table 14, Tathra-Disaster Bay area), Montgomery's (1983) and the present study. Data from Fairbridge were fitted using the BMDP non-linear estimation package. Montgomery and present study results are reproduced as reported, and are compared using an F-test (Draper and Smith, 1979). Comparison with Fairbridge was not possible due to the poor fit of the model to the data. RSS: residual sum of squares, RSSc: residual sum of squares for combined data set. Degrees of freedom in parentheses.

	K	L_{∞}	t_o	RSS	RSSc	F
Male						
Fairbridge	0.000006	660471.0	-5.221			
Montgomery	0.321	53.31	1.183	9.25(3)	6030.4(16)	63.90(3,13)
Present study	0.178	48.15	-1.687	373.7(10)		
						P < 0.005
Female						
Fairbridge	0.000093	58289.0	-3.476			
Montgomery	0.180	67.77	0.434	235.5(7)	8715.8(21)	95.81(3,18)
Present study	0.159	58.78	-1.220	278.1(11)		
						P < 0.005

TABLE 9. Male and female mean annular radii, +/- one standard deviation (SD), groups one and two combined.

	Annulus number	Mean radius (mm)	Mean radius +/- 1 SD (mm)
Male	1	2.046	1.494 - 2.598
	2	3.577	2.811 - 4.343
	3	4.934	4.212 - 5.656
	4	5.792	5.145 - 6.439
	5	6.299	5.754 - 6.844
	6	6.763	6.202 - 7.324
	7	7.182	6.652 - 7.712
	8	7.549	7.034 - 8.064
	9	7.820	7.316 - 8.324
	10	8.211	7.610 - 8.812
	11	8.582	8.064 - 9.100
	12	8.705	8.553 - 8.857
	13	8.898	8.730 - 9.066
Female	1	2.065	1.483 - 2.647
	2	3.553	2.784 - 4.322
	3	5.045	4.294 - 5.796
	4	6.084	5.369 - 6.799
	5	6.886	6.213 - 7.559
	6	7.524	6.899 - 8.149
	7	8.052	7.438 - 8.666
	8	8.526	7.919 - 9.133
	9	8.891	8.316 - 9.466
	10	9.156	8.641 - 9.671
	11	9.477	8.954 - 10.000
	12	9.614	9.100 - 10.128
	13	9.788	9.444 - 10.132
	14	10.424	9.906 - 10.942

FIGURE CAPTIONS.

FIG. 1. Otolith from tiger flathead, note hyaline and opaque zones.

FIG. 2. Standardised %EMI (see text), mean +/- one standard deviation plotted against time (month) for tiger flathead. 1983 and 1984 data for males and females combined. Males: age classes 4 - 6, females: age classes 4 - 7.

FIG. 3. Von Bertalanffy growth in length curves for male (top) and female (bottom) tiger flathead. The length-frequency distribution at each age class, fitted growth function and 95% confidence limits around the fitted line are shown.

FIG. 4. Approximate 95% confidence regions for L_{oo} and K for female (upper ellipse) and male (lower ellipse) tiger flathead.

FIG. 5. Comparison in growth of tiger flathead between 1. Dakin (1939, 2. Fairbridge (1951), 3. Montgomery (1983) and 4. present study. Male growth functions (top) and female (bottom) are shown. Dakin did not distinguish between sexes and provided a range in body length only, and these length ranges are shown on both plots. The von Bertalanffy function has been fitted to Fairbridge's (op. cit.) data from Table 14 for the Tathra-Disaster Bay area. Montgomery's and the present growth functions are plotted as reported.

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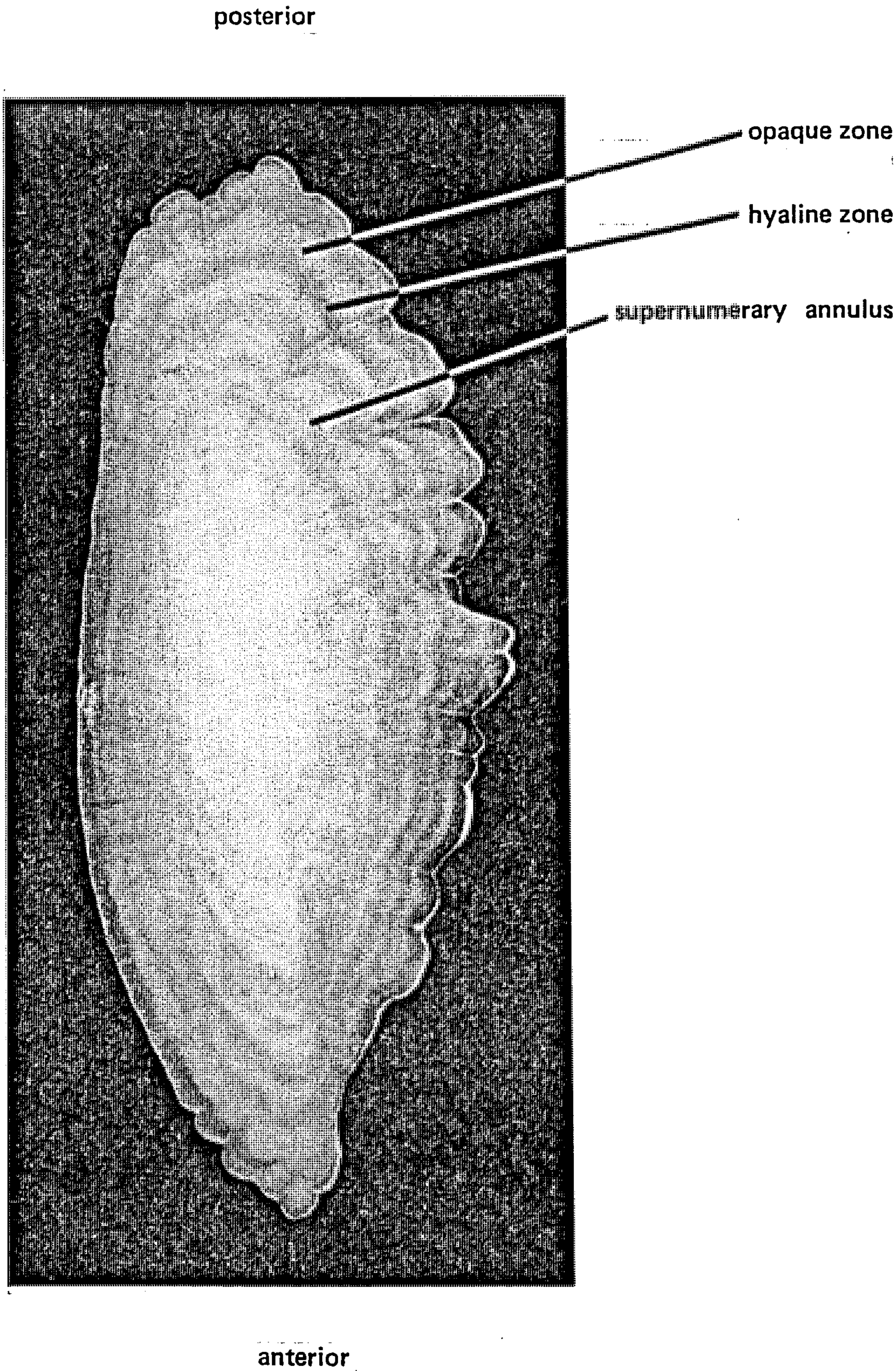
posterior
opaque zone
hyaline zone
supernumerary annulus
anterior

Figure 1.

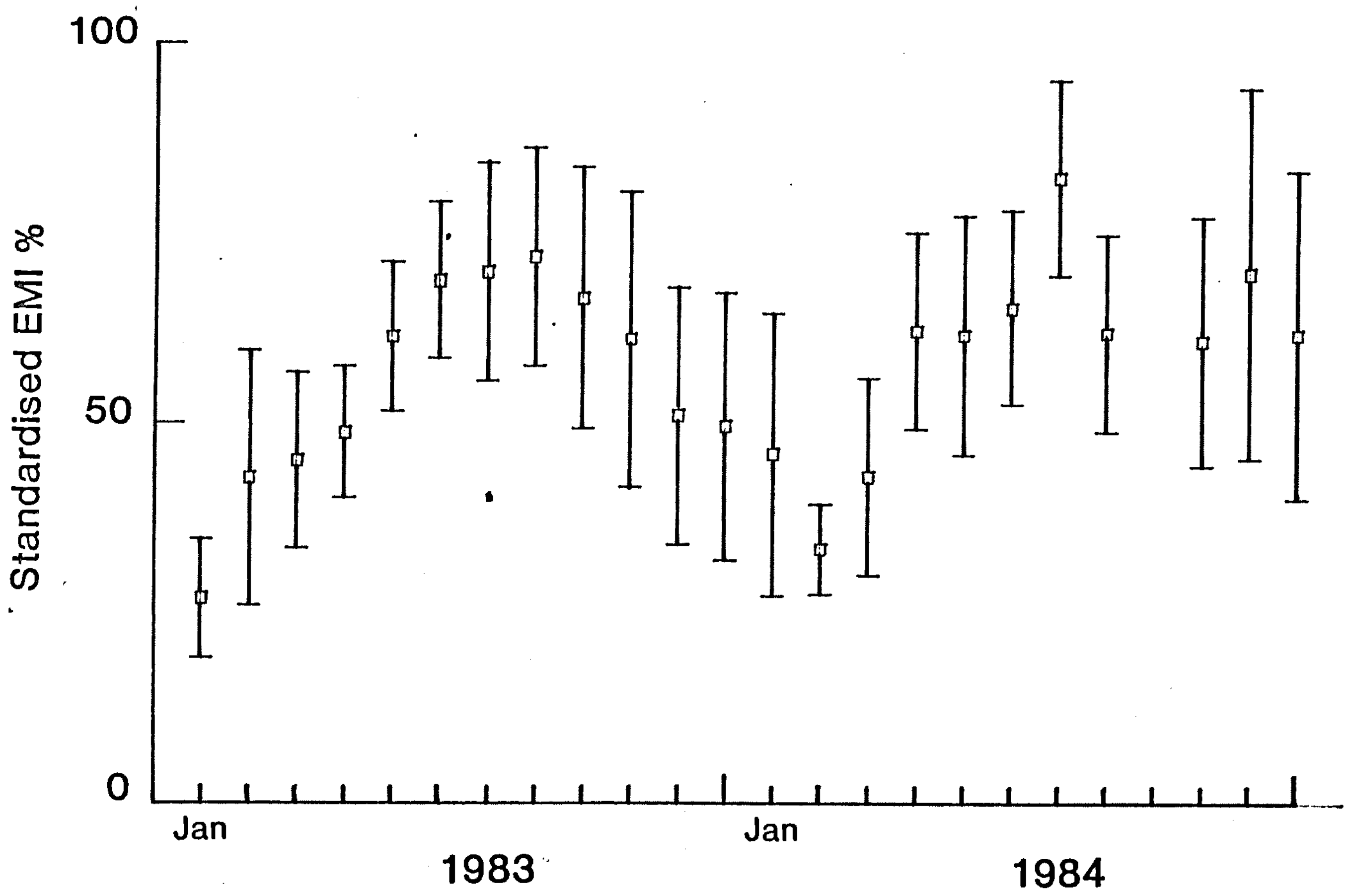

Figure 2.

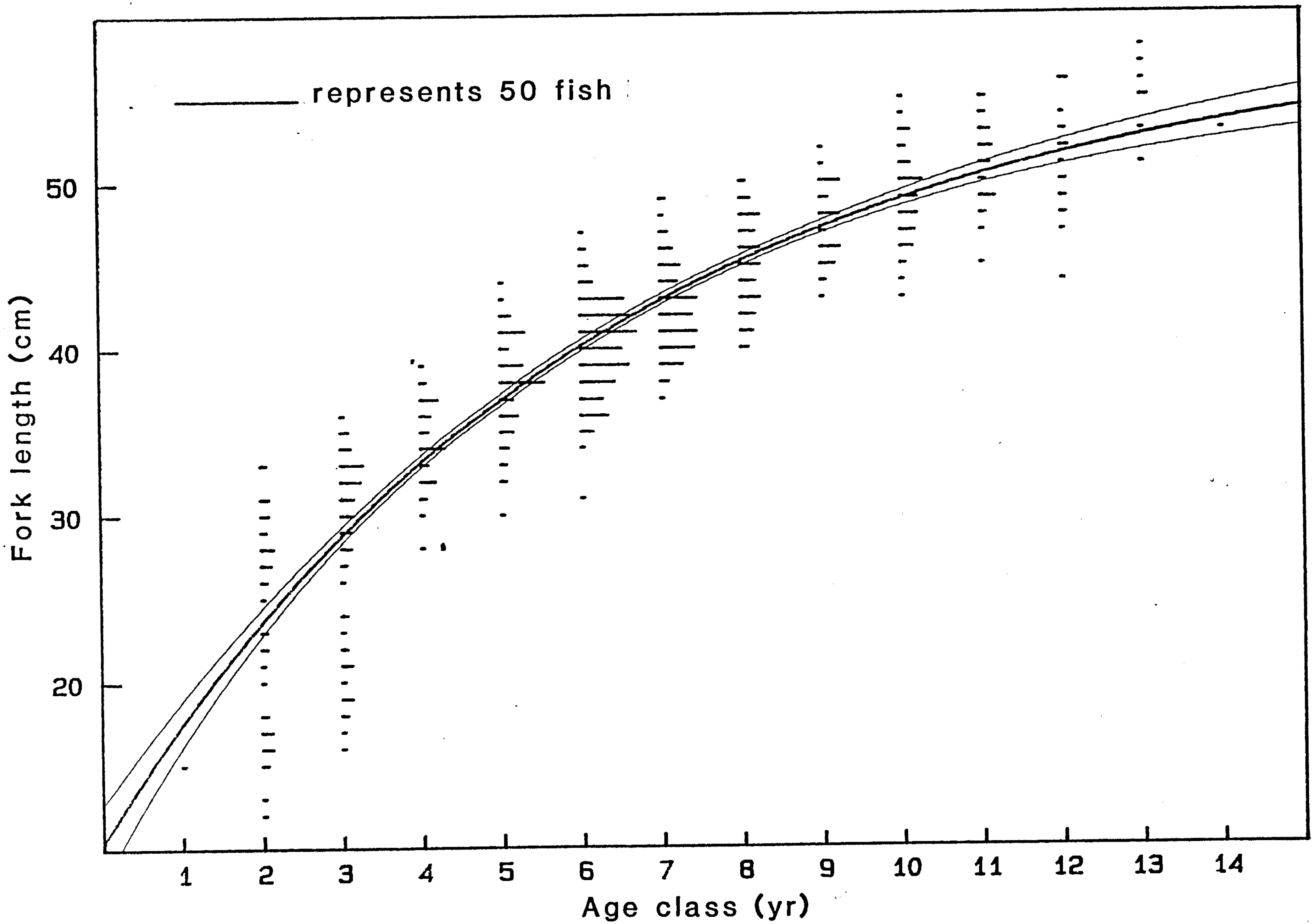
represents 50 fish
Fork length (cm)
50
40
30
20
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Age class (yr)

Figure 3.

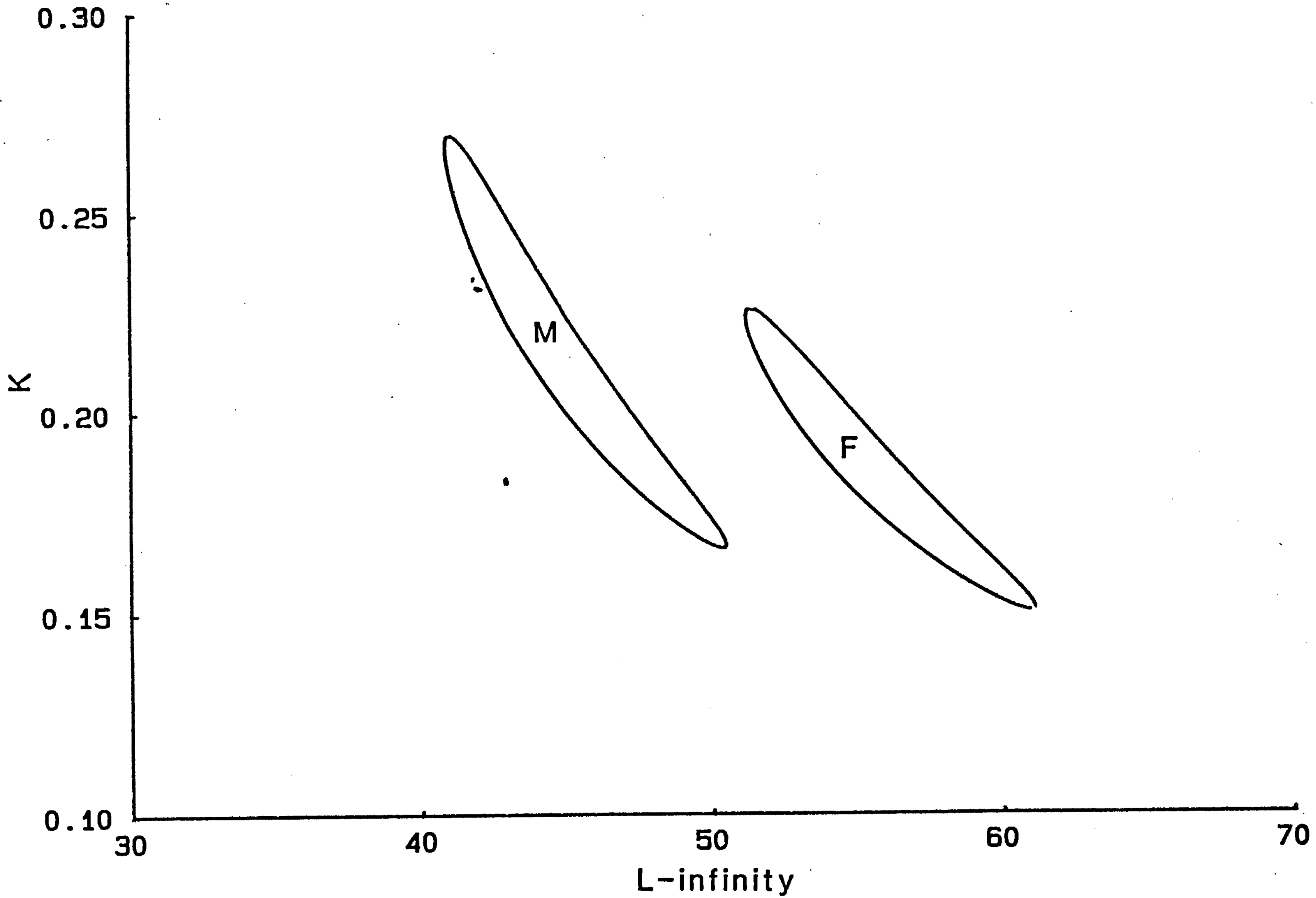

Figure 4.

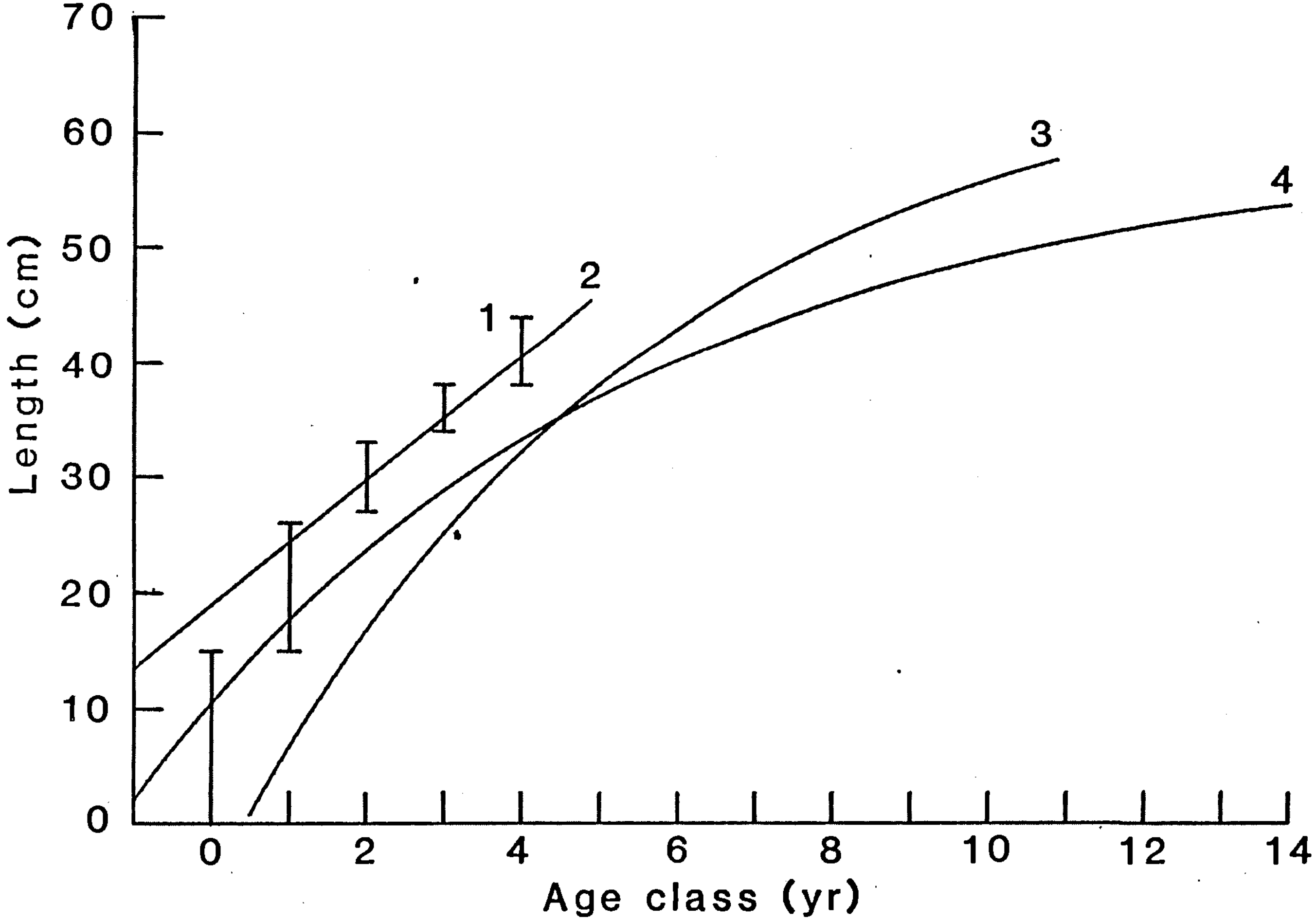

Figure 5.

Female TF