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Back-calculation of the growth of capelin (Mallotus villosus) in the Newfoundland area[1]

by

G. H. Winters
Department of the Environment
Fisheries and Marine Service
Biological Station
St. John's, Newfoundland.

Introduction

Due to its relatively minor importance as a commercial species, previous research on capelin in the Northwest Atlantic has tended to be intermittent and restricted to the Newfoundland area. Among the most notable works are those by Jeffers (1931) who dealt mainly with larval development, Sleggs (1933) who concentrated on its economic biology, Templeman (1948) who elucidated many aspects of its life history, and Pitt (1958a, 1958b) who provided information on age, growth, distribution, spawning and racial aspects of capelin. Although the growth history of the inshore capelin and the Grand Bank capelin has been adequately described by Templeman (1948) and Pitt (1958a), respectively, there has been no comparison of the growth rates of capelin from other areas of its range in the Canadian Northwest Atlantic. In view of the recent development of an expanding offshore fishery for capelin this paper presents new information on the variations in growth of capelin in the Newfoundland area.

During 1966-72 the author obtained samples of capelin from a wide range of localities in the Newfoundland area. These samples consisted mainly of mature or maturing fish and were taken from the various areas at different times during the year. As a result, growth curves based on lengths at capture would be incomplete for the younger ages and, also, comparison of growth curves among the different areas would not be strictly accurate due to varying amounts of new (current) growth. To overcome these difficulties the author utilized the back-calculation technique which not only provides an estimate of growth for those earlier ages not available but also defines the period of growth for comparative purposes.

The back-calculation technique has normally been applied to scale measurements but in capelin the first growth ring is usually missing on the scale (Templeman, 1948) and the annuli are not well-defined. Consequently otoliths were selected for measurement. Back-calculation of capelin growth from otolith measurements has been carried out previously by Templeman (1948, 1968) for the Newfoundland area and by Prokhorov (1965) for the Barents Sea area. Templeman (1948) measured otolith widths but did not establish the form of the otolith width-fish length relationship and instead back-calculated fish lengths from direct otolith width-fish length ratios. Templeman (1968) determined that the otolith width-fish length relationship was in the form of two straight lines and back-calculated capelin lengths from the empirical lines. However, he did not separate the sexes or areas in determining the form of the otolith width-fish length relationship. Prokhorov (1965) measured otolith radii and found that the otolith radius-fish length relationship in capelin was in the form of an irregular curve which was different for each sex.

Materials and Methods

Source of samples

The material was obtained from widely distributed localities from Fortune Bay (Fig. 1) to Davis Inlet, Labrador and includes both beach-spawning coastal capelin and bottom-spawning offshore capelin as well as immature, pre-spawning, spawning and spent groups of capelin. Beach-spawning capelin from Pack's Harbour, Outer Cove, and Grand Beach were caught by small-meshed (10-20 mm) castnets. Pre-spawning and

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spent capelin from the Southeast Shoal of the Grand Bank were caught by the research vessel A. T. Cameron using a No. 41 Yankee otter trawl with a 24-metre headline and a codend liner ranging from 10-30 mm in stretched mesh dimension. Pre-spawning capelin from Trinity Bay were caught by the A. T. Cameron with 30 mm mesh in the liner of the otter trawl. Immature capelin from Trinity Bay were caught by the research vessel Investigator II using a No. 4 mid-water trawl with a mouth opening 6 metres square and a 10 mm liner in the codend. Gillnets with mesh sizes ranging from 20 to 40 mm were used to catch spawning capelin in Trinity Bay. The Notre Dame Bay samples were kindly provided by the Soviet research vessel Persey III.

Methods of fish measurement and conversion of preserved lengths

For convenience and rapidity in measuring capelin, only the greatest total lengths (in millimetres) were used, i.e. from the tip of the mandible to the end of the ventral lobe of the caudal fin deflected back in a straight line with the body (Templeman, 1948).

Because many of the samples were frozen, either dry or in seawater, it was necessary to determine the shrinkage factor for conversion of thawed lengths to fresh lengths. Two samples of capelin of approximately 100 fish each were measured fresh, tagged and placed in two separate bags, one empty and the other containing seawater, and frozen. After one week these were thawed in water and measured again by the same person. Regression lines of fresh length on thawed lengths were then determined and these are shown in Fig. 2. There is very little difference in shrinkage between those capelin frozen in seawater and frozen dry. The shrinkage over the length range represented is approximately 3% and this factor was used to convert thawed lengths to fresh lengths. Lengths of capelin preserved in 95% alcohol were increased by 5% (Winters, MS 1966).

Age determination and otolith measurements

For age determinations the otoliths were placed in a black watch-glass and immersed in 95% isopropyl alcohol. A stereoscopic model SMZ Nikon microscope with a micrometer in one eyepiece was used to examine the otoliths. Ages were determined from the lateral convex face of the otoliths and involved two methods, the main method utilizing the alternate opaque summer and translucent winter bands, and the corroborating method utilizing the ridge and groove technique as described by Templeman (1948). All otoliths with poorly defined annuli were omitted in age determinations.

Otolith radii were measured instead of otolith widths because radii are easier and more convenient to measure and also new growth is apt to appear first at the ventral edge of the otolith particularly in older fish. The otolith was aligned such that there was a straight line AB extending from the rostrum to the centre of the first year (Fig. 3). Then the radius of the otolith to the outside of each winter ring was measured by the ocular micrometer along BC at right angles to AB. The otolith radii were read in terms of eyepiece units (1 mm = 26.5 EPU). All otoliths with irregular or abnormal shapes were not measured.

Results

Relation of otolith radius to fish length for Trinity Bay capelin

All ages and maturity stages for both sexes were represented in the Trinity Bay samples. Consequently Trinity Bay was selected as the main area for the description of the relationship of the otolith radius to the total length of capelin (subsequently termed the otolith-body relationship).

The increasing disparity in size existing between the sexes after their first year of life (Templeman, 1948; Pitt, 1958a) necessitated the separation of sexes in determining the otolith-body relationship of capelin 2 years old and older. The otolith radius measurements were grouped in intervals of 0.5 EPU and average body lengths in mm were plotted at the midpoint of each otolith radius interval. The freehand curves (Fig. 4) indicate that the otolith-body relationship in capelin is in the form of an irregular curve which is different for each sex. The shape of the curves and the crossing over of the curves of males and females is similar to that established by Prokhorov (1965) for Barents Sea capelin. The inflexion points occurring at 165 mm for males and 150 mm for females represent the approximate average size at maturity for each sex. Templeman (1968) noted that the intersection point of the two straight lines describing the relationship between the otolith width and total length of capelin represented the approximate size of maturity for both sexes.

Transformation of the data to natural logarithms failed to produce an otolith-body relationship amenable to convenient mathematical description. Consequently back-calculation of body lengths from otolith annuli measurements of capelin was carried out by reading off fish lengths corresponding to otolith radii from the empirical curve of the otolith-body relationship of Fig. 4.

Age-length relationship of Trinity Bay capelin

For each age-group lengths were back-calculated to the end of the last winter zone, averaged and plotted against age for males and females. (Fig. 5a) (Table 1). Comparisons of the growth curves of capelin which are mature at age 3 indicates that the greater acceleration in the growth rate of males relative to females after age 1 produces a maximum size disparity (30 mm) at age 3 after which the size difference declines to approximately 20 mm. Immature capelin at age 3 are considerably smaller than mature capelin of the same age, the difference being in excess of 40 mm for males and in excess of 30 mm for females.

The age-length relationship of capelin was also obtained by averaging the back-calculated lengths of all fish at each age (Fig. 5b). These curves represent the average of the former sizes of those fish that have survived to the sampling age and according to Ricker (1969) are more representative of the true growth rate than are the length-at-capture curves. Thus Fig. 5b indicates that the size disparity between the sexes increases up to a maximum (23 mm) at age 3 and decreases slightly thereafter.

Growth patterns of successive age-groups

Lengths at previous annuli for age-groups 3-6 in Table 1 were plotted against age for male and female capelin in Trinity Bay (Fig. 6). For both sexes there is an initial divergence in the growth curves of successive age-groups followed by an apparent convergence after age 3. According to Zamakhaev (1965) this initial divergence and subsequent convergence of the growth curves of successive age-groups is characteristic of Lee's phenomenon of apparent change in growth rate with age in its typical form. Comparison of back-calculated lengths for ages 1-6 (Table I) indicates that Lee's phenomenon is clearly present at all ages in the mature fish but is not well defined in the immature fish. Inasmuch as the immatures at age 3 must mature at some age older than 3, it is clear that they also must show Lee's phenomenon because they are smaller than mature 3 year-olds at successive annuli.

The later convergence of the initially diverging growth curves shown in Fig. 6 may sometimes be regarded as the phenomenon of growth compensation between successive age-groups (Zamakhaev, 1965). In view of this, computed year-old lengths (L_1 values) of fish of age-groups 4 and 5 were divided into length groups arranged in increasing magnitude of size and their increments in subsequent annuli and final lengths were compared (Table 2). Both male and female 4-year-old capelin show distinct growth compensation during their second year with the specimens having the smallest L_1 values having the largest increments and vice versa. This pattern however is reversed during the third year with the initially faster growing fish having the largest third year size increment. This corresponds to the age of maximum size difference between mature and immature capelin as shown previously in Fig. 6. Growth compensation is again evident during the fourth year of the 4-year-olds with the result that the initial size spread at age 1 is substantially reduced by age 4.

For 5-year-olds growth compensation is very pronounced in both males and females during their second year. It is less pronounced after age 2 in the males whereas the females show a similar pattern to the 4-year-olds in that the initially fast-growing fish exhibit the largest increment at age 3 and the smallest increment for the other ages. Nevertheless by age 5 growth compensation has virtually eliminated the superiority in length of the fast-growing fish at the end of the first year's growth.

Otolith-body relationship of other areas of the Northwest Atlantic

Since the samples from the other areas of the Northwest Atlantic consisted mainly of mature fish and represented only a restricted length-range, it was not feasible to compare the empirical curves of the otolith-body relationship for these areas. Instead ratios of the otolith radius to the total length of mature fish of each sex were compared (Table 3). There are no consistent differences existing in the otolith-body ratio among the various areas. Consequently, lengths at previous ages of fish from the other areas of the Northwest Atlantic were back-calculated from the empirical curve established for the otolith-body relationship of Trinity Bay capelin (Fig. 4)

Comparison of growth

For each of the ages of mature fish available; lengths at previous annuli were computed for each area and an average length was calculated for each annulus. The growth curves of the various areas the data were analyzed according to the von Bertalanffy (1938) growth equation;

$$l_t = l_\infty (1 - e^{-k\ (t-to)})$$

when l_t is mean length at age t years, L_∞ is the asymtotic length, K is a constant determining the rate of change in length increment, and t_o is the theoretical age at zero length. Growth curves based on average length at age were fitted using the method of Allen (1966).

The von Bertalanffy growth equation may be used to describe the growth patterns of capelin in the Northwest Atlantic (Fig. 7). With the exception of the Pack's Harbour sample L_∞ values derived from the growth data of each area correspond fairly well to the maximum length obtained in the area.

The growth curves of the various areas are compared with each other in Fig. 8. There are several patterns of growth evident from these curves: i) the Trinity Bay, Outer Cove, Grand Bank and Grand Beach capelin, representing the central part of the capelin range in the Canadian Northwest Atlantic have a similar growth pattern and contain fish with a fast growth rate and large average size at age, particularly in fish less than 5 years old; ii) the Labrador (Pack's Harbour) capelin representing the northern part of the capelin's range have a small length at age in their younger years but whose growth rate relative to that of the east coast and Grand Bank capelin accelerates with age to produce as large a maximum size; iii) the Notre Dame Bay capelin, intermediate in geographical location between the Grand Bank areas and eastern Labrador have also an intermediate growth late; iv) the very large size disparity (35-40 mm) among the various areas at age 1 is substantially diminished by ages 5 and 6 (approximately 10 mm). This is analogous to the growth pattern of the various age-groups in Fig. 6 and may be considered to represent growth compensation between areas.

Length-frequency curves of immature 2 year-olds (Fig. 9a) illustrate the increase in size from Davis Inlet south to Avalon Channel. The difference in size between the Henley Harbour and Davis Inlet samples and those from Trinity Bay and Avalon Channel are actually larger than shown because of the greater amount of new growth observed in the otoliths of the Labrador capelin which were caught 1-2 months later. At age 5 (Fig. 9b) there is very little difference in the size distribution of Pack's Harbour capelin and those from the east coast of Newfoundland and Grand Bank.

Discussion and Conclusions

A gradual change has been demonstrated in the growth pattern of capelin from the north to the south of the range in the Newfoundland-Labrador area, i.e. a large final size which is approached rather slowly in the Labrador area; a slightly smaller final size which is approached rapidly in the Grand Bank area; and intermediate values of these parameters in capelin from Notre Dame Bay. This north-south cline in capelin growth can undoubtedly be attributed to the hydrography of the area under consideration. The Labrador current dominates the temperature regime of the Newfoundland area (Smith et al, 1937; Dunbar, 1951; Bailey and Hachey, 1951; Hachey et al, 1954) and the volume of cold water carried by the Labrador current declines from north to south (May et al, 1965). Mass beach-spawning of capelin in the Newfoundland area is determined mainly by the availability of suitable and specific temperatures required for spawning. These temperatures range from 5.5-8.5°C (Templeman, 1948; Winters, MS 1966). On the south coast of Newfoundland (Fortune Bay) such temperatures are generally reached by the first or second week in June (Templeman, 1948). Along the east coast of Newfoundland beach-spawning usually begins around the middle of June in the Conception Bay area and by late June-early July in the Notre Dame Bay area. In southern Labrador mass beach-spawning usually does not begin until early July and may extend to mid-August (Templeman, 1948). In northern Labrador beach-spawning may not begin until mid-August. Recent surveys of the southeast shoal of the Grand Bank, where demersal spawning of capelin occurs, suggests that spawning begins there around mid-June, although Pitt (1958a) reported that spawning occurred there as late as August in 1950. He attributed this late spawning to the unusually cold temperatures over the southeast school area in 1950.

The spawning period of capelin thus begins progressively later from south to north in the Newfoundland-Labrador area and this difference may amount to as much as 1½-2 months in the extremes of the area under consideration. As a result there is therefore a gradual attrition in the duration of the growing period during the first year of growth from south to north and this is undoubtedly reflected in the progressive decrease in L_1 values from the Grand Beach-Grand Bank area to Labrador (Fig. 8). For example capelin average about 78 mm after their first year in Fortune Bay compared to 41 mm in the Pack's Harbour area. This disparity in size at age is reflected in the age composition of mature fish from the particular areas (Table 4). Labrador capelin would appear to mature about a year later on the average than Grand Bank capelin and contain fewer representatives at the younger ages.

In the context of the influence that growth in the first years of life has on subsequent growth, the phenomenon of growth compensation is of special interest in fish, and various explanations for its occurrence as a biological phenomenon have been given in the literature (Watkins, 1927; Runnstrøm, 1936; Smith, 1956). According to Zamakhaev (1965), Lee's phenomenon in its typical form may sometimes be regarded as the same thing as growth compensation. Naturally then, in such cases, they will have the same cause.

The occurrence of Lee's phenomenon in capelin is a property of its life history biology particularly with reference to its spawning characteristics. The older capelin and the larger individuals of a year-class tend to spawn first and, particularly so for the males tend to remain on the spawning grounds for prolonged periods of time (Templeman, 1948). Since capelin are known to suffer a high spawning mortality one would therefore expect the greatest mortality to be in the older and larger individuals. This is demonstrated by comparing the percentage age compositions and mean length at age of pre-spawning and post-spawning (spent) capelin caught on Grand Bank in June and August, 1967 (Table 5). Spawning mortality is greatest for the older fish and for the larger individuals of a year-class and as a result the survivors of spawning consist mainly of younger and smaller fish. Prokhorov (1960) found similar results in spent capelin from the Barents Sea. Thus as a year-class gets older the proportion of slow-growing will increase and consequently lengths at previous ages as back-calculated from older fish will be smaller than the average size of those fish that have survived to and are sampled at these previous ages. Since only a small proportion of capelin mature to spawn at age 2, size selective mortality would not have a significant effect at this age and both slow and fast growing 2-year-olds would be expected to survive in approximately equal proportions to age 3. This probably accounts for the lack of evidence for Lee's phenomenon at age 2 in Table 1.

The growth compensation in capelin that occurs within a age-class probably results from differing ages at maturity of initially fast-growing and slow-growing fish. Capelin which have attained a large size at the end of their first year would be expected to mature at an earlier age than the smaller individuals. This is reflected in the larger L_1 values associated with mature 3-year-olds relative to mature 4-year-olds in Fig. 6 and similarly with mature 4-year-olds relative to mature 5-year-olds. The spawning process in capelin is associated with cessation of feeding (Templeman, 1948; Winters, 1970) and with deterioration in body conditions (Winters, 1970). Consequently, maturation and spawning must result in some retardation in growth of capelin as has been generally demonstrated for a variety of species. Since immature capelin do not suffer this retardation in growth they would be expected to grow more rapidly than their cohorts who undergo spawning at that particular age. This would eventually enable the initially slow-growing fish to achieve equality in length with the initially fast-growing fish and would result in growth compensation as exhibited in Table 2. This is analogous to the convergence of the growth curves between areas (Fig. 8) which may be attributed to the differing ages at maturity of fish with large L_1 value in the Grand Bank area and those with small L_1 values in Labrador. The reversal of growth compensation in ages 3 and 4 in Table 2 may be attributed to the possible acceleration of growth of capelin during their maturation year. For example during their third year mature 3-year-old males produced a growth increment of 54 mm compared with only 29 mm for immature males of the same age (Table 1).

There is some evidence to suggest that a portion of the Grand Bank capelin move inshore to spawn. Templeman and Fleming (1962) report that cod tagged on the northwest part of Grand Bank in early June were recaptured on the Avalon Peninsula in late June during the capelin spawning period in that area. Since these cod were feeding on capelin at the time of tagging it seems likely that the cod followed the capelin from the Grand Bank to shore. Dragesund and Monstad (1973) provide evidence from acoustic surveys of the Grand Bank area to suggest that a portion of the capelin on the western and southwestern part of Grand Bank also move westward and inshore to spawn. The similarities in growth rates of the Fortune Bay, Avalon Peninsula and Grand Bank capelin may therefore reflect such stock interrelationships.

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Table 1. Back-calculated lengths of Trinity Bay capelin as determined from the empirical curve of the otolith-body relationship shown in Fig. 4.

Age at Capture	Sex	Maturity	No. of fish	Length at capture (mm)	Computed size at successive annuli (mm)					
					1	2	3	4	5	6
1	Juv	Imm	76	78	73					
2	M	Imm	82	115	76	115				
	F	Imm	150	112	74	111				
3	M	Imm	52	141	70	112	141			
	F	Imm	25	127	68	103	124			
3	M	Mat	77	187	81	131	186			
	F	Mat	43	159	78	117	155			
4	M	Mat	176	201	76	118	170	200		
	F	Mat	61	180	74	110	158	180		
5	M	Mat	76	203	69	111	137	183	203	
	F	Mat	141	184	70	107	130	173	183	
6	M	Mat	5	205	66	109	133	178	201	205
	F	Mat	5	184	67	99	117	150	177	184
	M			Average	74	118	162	194	202	205
	F			length	72	109	139	174	183	185

Table 2. Subsequent growth of Trinity Bay capelin in relation to their length at the end of the first year (L_1).

Age at capture	Males						Females					
	L_1 (mm)	Length increments(mm) at age				Final size	L_1 (mm)	Length increments(mm) at age				Final size
		2	3	4	5			2	3	4	5	
4	56	51	35	50		192	56	48	43	30		177
	64	49	34	49		196	64	44	46	27		181
	72	43	35	48		198	72	37	37	35		181
	78	37	40	43		198	78	37	45	23		183
	84	39	42	47		202	84	36	54	11		185
5	48	56	30	43	24	201	56	50	18	44	14	182
	56	52	28	44	22	202	64	42	19	43	14	182
	64	45	27	44	22	202	72	37	30	35	9	183
	72	40	27	41	22	202	78	36	26	40	4	184
	78	34	26	42	21	201	84	34	35	28	3	184

Table 3. Ratio of otolith radii (in EPU) to total length (in mm) of mature capelin from different localities in the Canadian Northwest Atlantic.

Midpoint of length interval (mm)	Notre Dame Bay		Grand Beach		Grand Bank		Trinity Bay		Outer Cove		Pack's Harbour	
	M	F	M	F	M	F	M	F	M	F	M	F
120												
125												
130					.169	.168						
135				.166		.163						
140				.163	.162	.168				.171		
145				.163	.170	.168		.171		.166		
150	.160	.162		.165	.163	.167		.167		.159		
155	.160	.158	.151	.163	.163	.166		.167	.161	.165		.155
160	.155	.159	.155	.156	.168	.161		.163	.166	.160		.158
165	.160	.157	.156	.156	.158	.161	.167	.160	.164	.158		.159
170	.155	.160	.157	.152	.160	.161	.168	.163	.165	.159	.159	.160
175	.152	.156	.154	.157	.163	.161	.154	.158	.160	.154	.149	.157
180	.154	.154	.158	.154	.161	.161	.157	.157	.158	.164	.152	.165
185	.156	.153	.153		.159	.155	.152	.150	.162	.159	.153	.158
190	.151	.150	.154		.154	.155	.151	.153	.158	.154	.151	.155
195	.155	.157	.151		.156		.156	.151	.155		.157	.154
200			.155		.148		.154	.153	.159		.153	.165
205					.156		.150		.151		.150	.154
210					.149		.146		.153		.154	
215							.149				.151	

A 8

Table 4: Age composition of mature capelin from various localities in the Canadian northwest Atlantic 1966-67. (A) males; (B) females.

	Percent at each age			
Age	Pack's Harbour	Trinity Bay	Outer Cove	Grand Bank
(A)				
22	-	-	-	0.3
3	0.6	19.5	39.3	65.7
4	36.3	62.6	50.6	31.1
5	55.0	17.5	9.3	3.0
6	8.1	0.4	0.8	-
Av. Age	4.71	3.99	3.72	3.38
(B)				
2	-	0.2	1.2	1.3
3	3.4	12.4	39.4	49.4
4	27.6	16.8	20.7	30.1
5	52.8	67.1	37.1	17.7
6	16.2	3.5	1.6	1.5
Av. Age	4.82	4.61	3.99	3.69

Table 5. Percentage age composition (A) and average length at age (B) (back-calculated to the end of the last winter zone) of mature pre-spawning and spent capelin from the Grand Bank, 1967.

	Males						Females					
		Age at capture						Age at capture				
Maturity condition	2	3	4	5	6	Average Age	2	3	4	5	6	Average Age
A												
Pre-spawning	0.3	65.7	31.1	3.0		3.38	1.3	49.4	30.1	17.7	1.5	3.69
spent	27.4	50.0	17.9	3.5	1.2	2.96	12.3	72.1	12.3	3.2		3.09
B												
Pre-spawning	161	178	191	198	-		133	162	173	180		
spent	150	172	184	194	204		132	153	166	170		

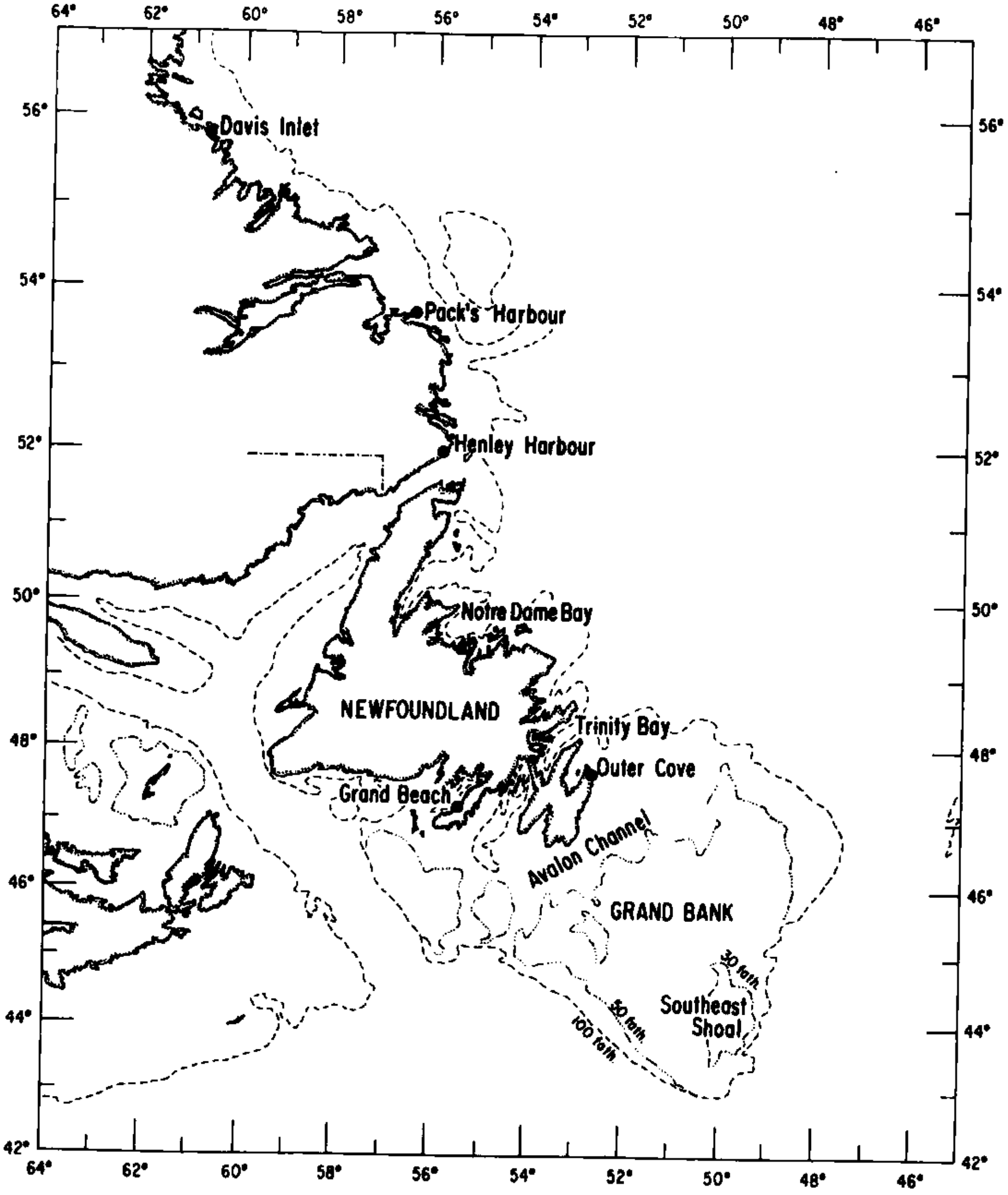

Fig. 1. Area map showing place names and localities mentioned in the text.

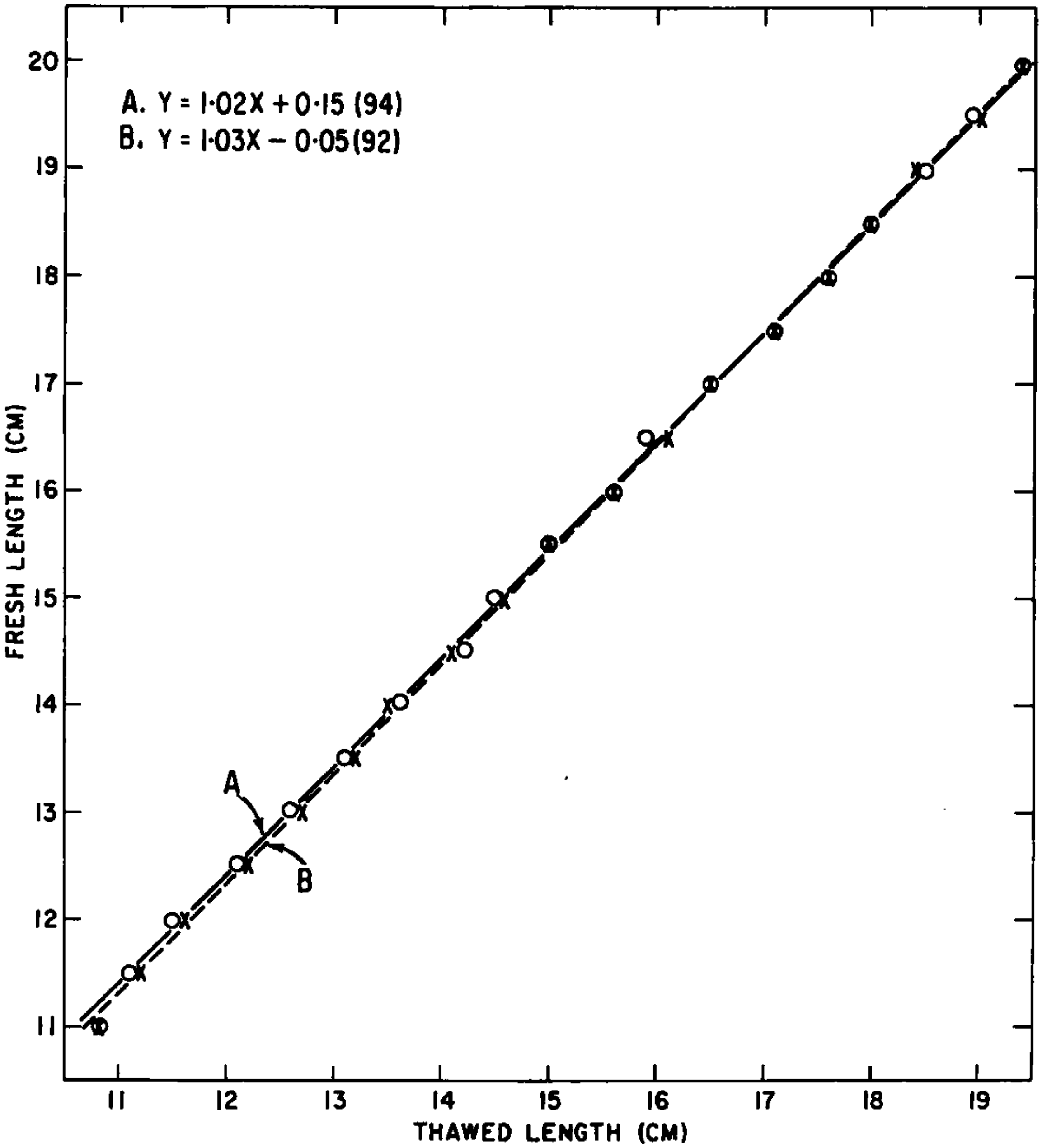

Fig. 2. Regression lines of fresh length on frozen (thawed) length of capelin frozen in brine (A) and dry (B).

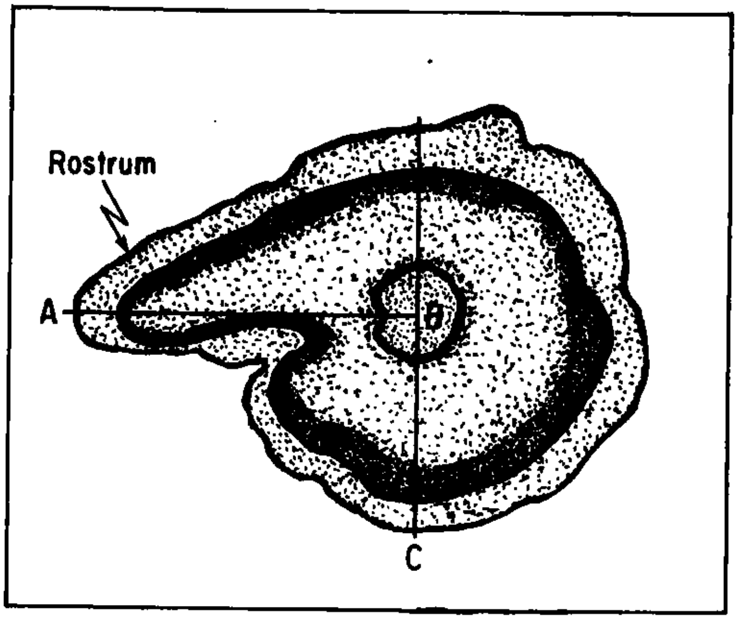

Fig. 3. Sketch of capelin otolith indicating the manner in which otolith measurements were made.

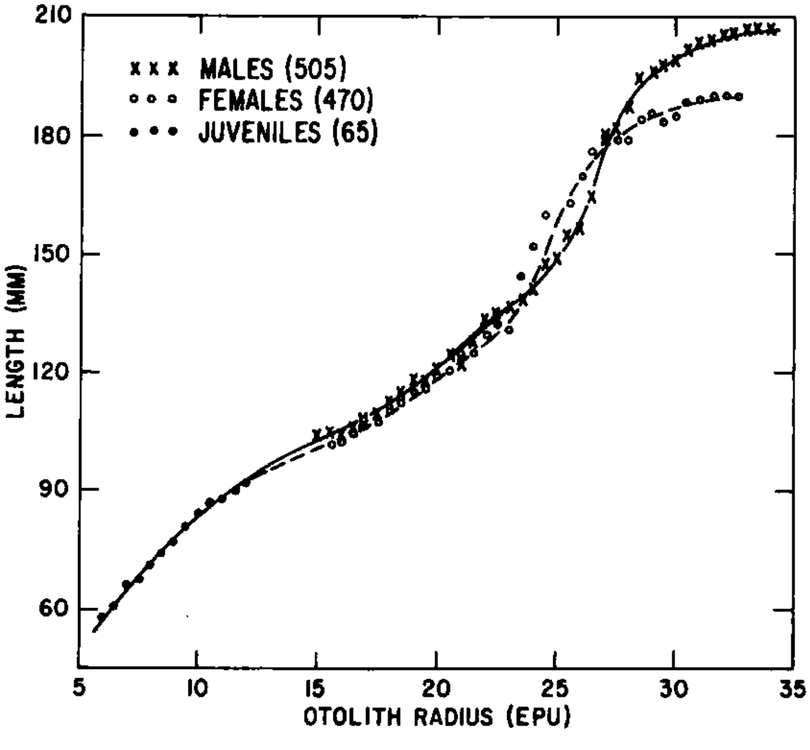

Fig. 4. Relationship between fish length and otolith radius for Trinity Bay capelin.

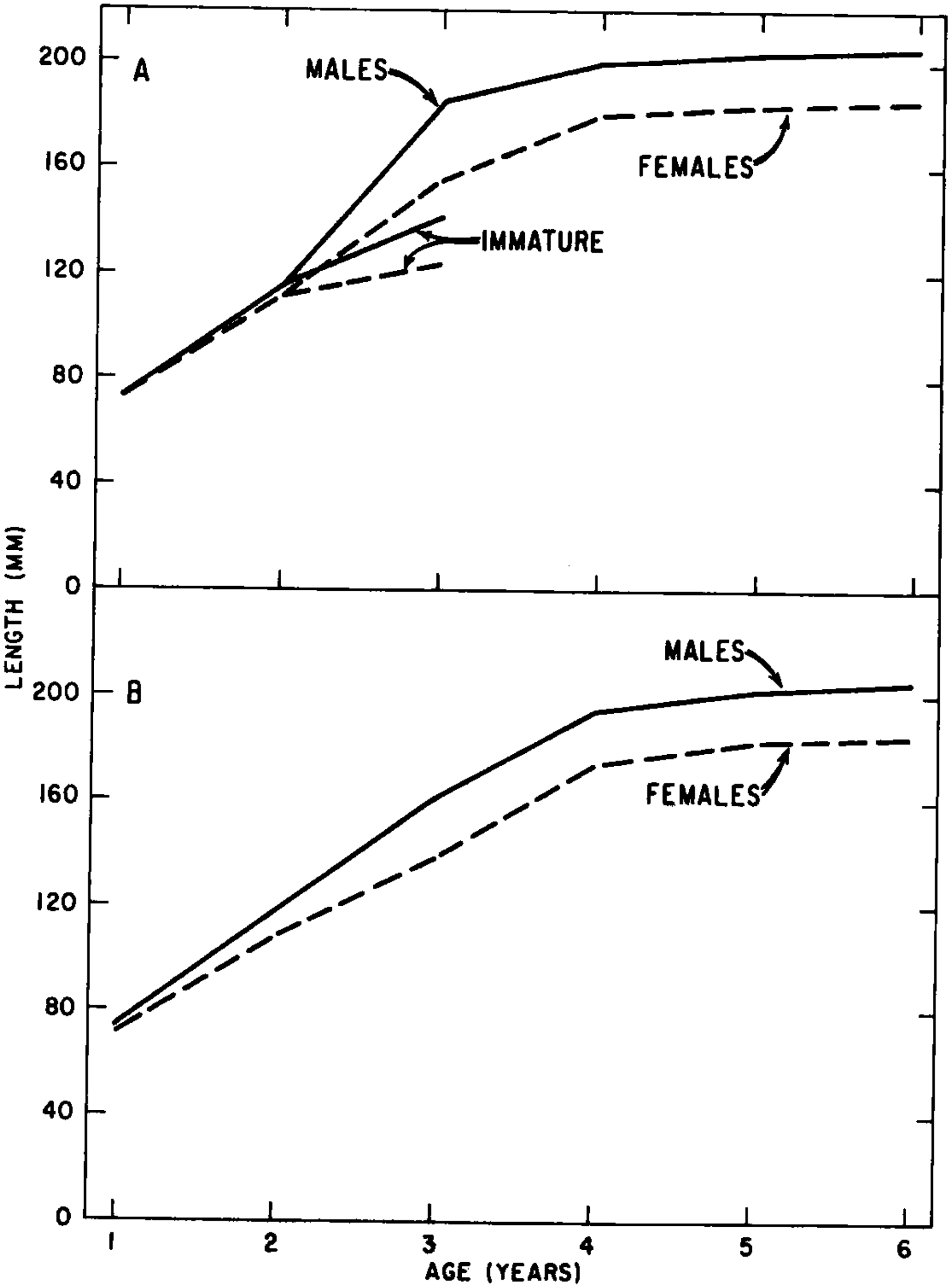

Fig. 5. Growth curves of Trinity Bay capelin. (A) represents average lengths (back-calculated to the end of the last winter zone) as age of capture, and (B) represents the average of the back-calculated lengths of all fish surviving to a particular age.

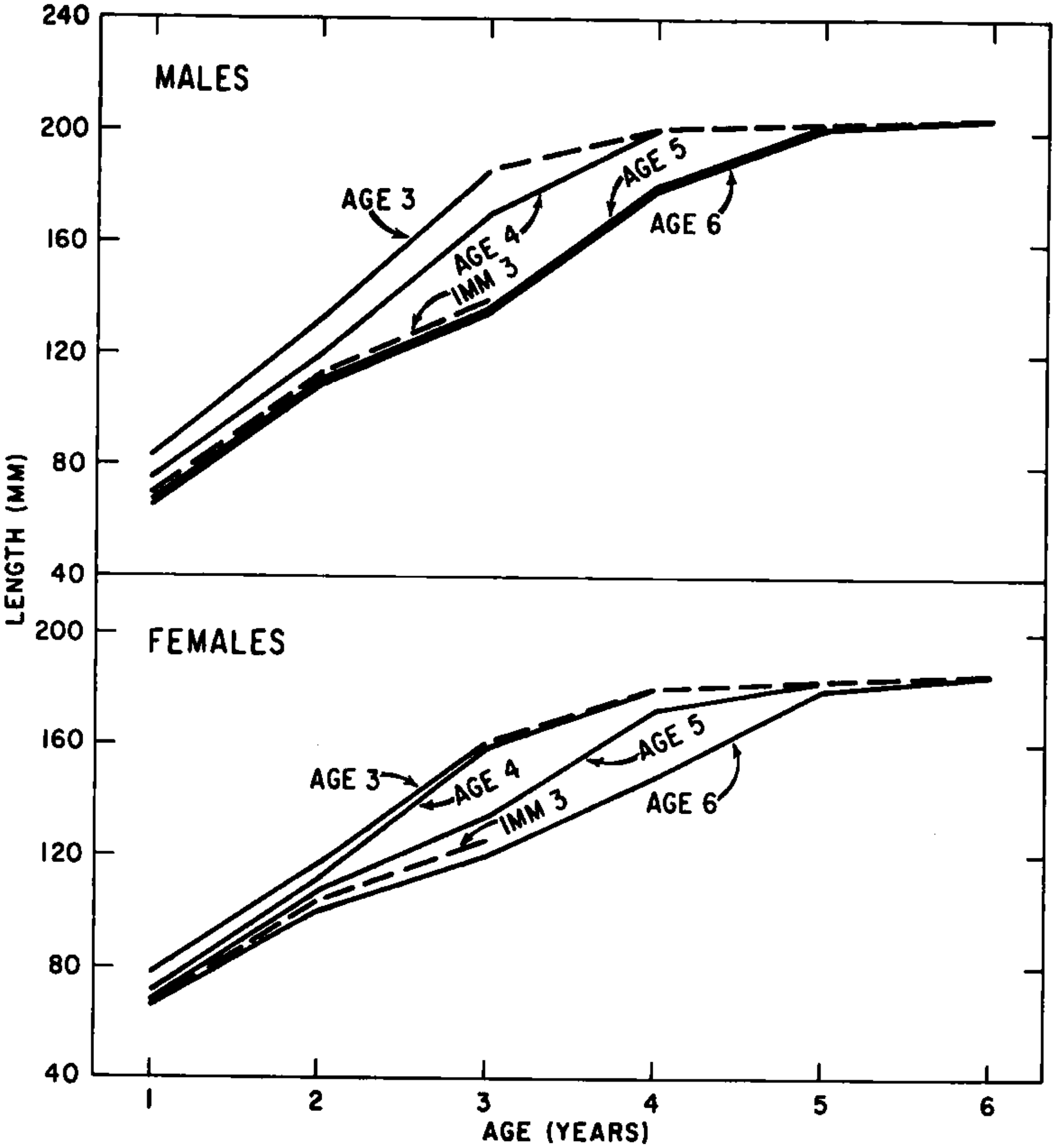

Fig. 6. Growth curves of successive age-groups of Trinity Bay capelin as determined from back-calculated lengths.

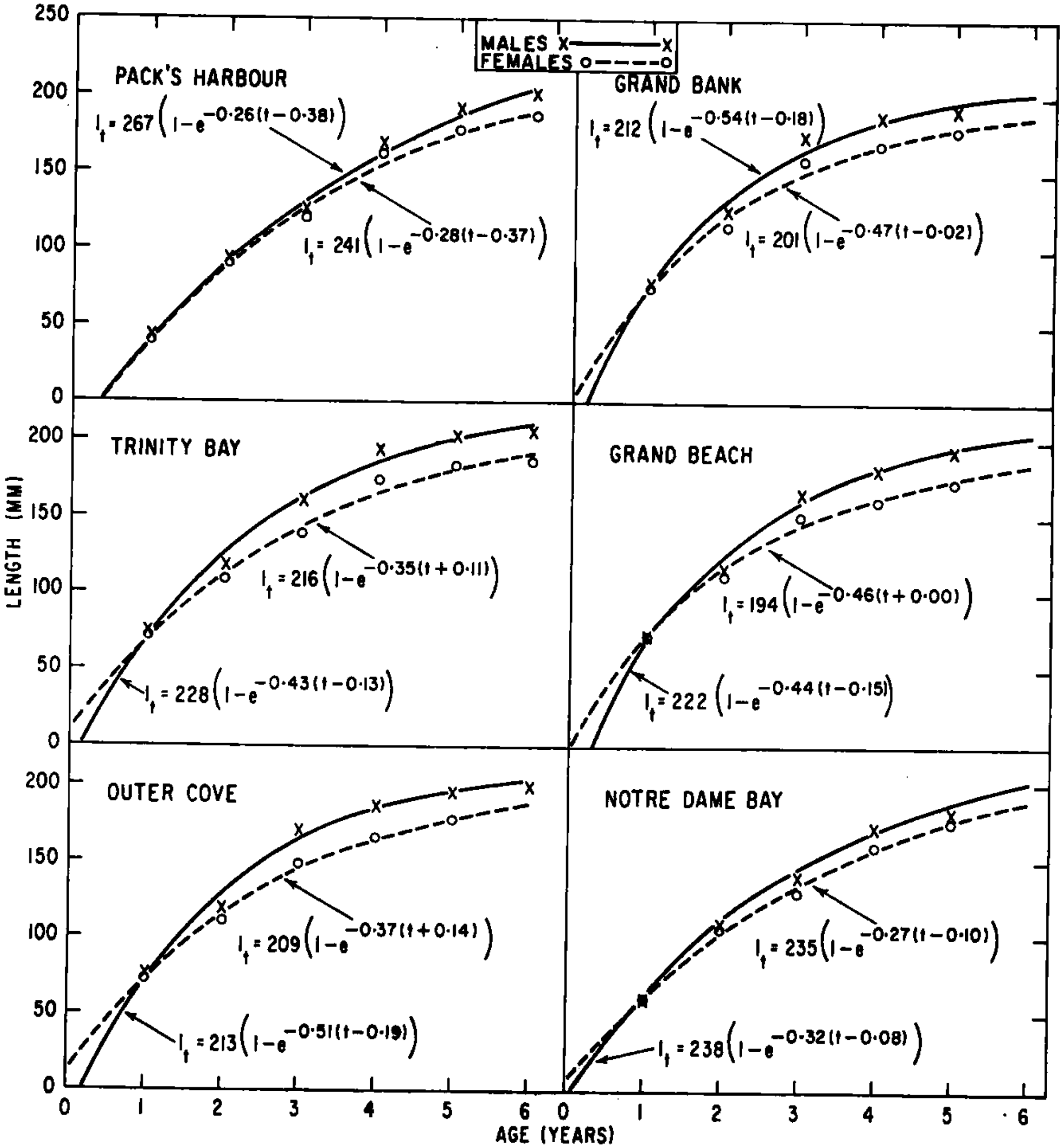

Fig. 7. Growth curves of capelin from various areas in the Newfoundland-Labrador area as fitted by the von Bertalanffy growth equation.

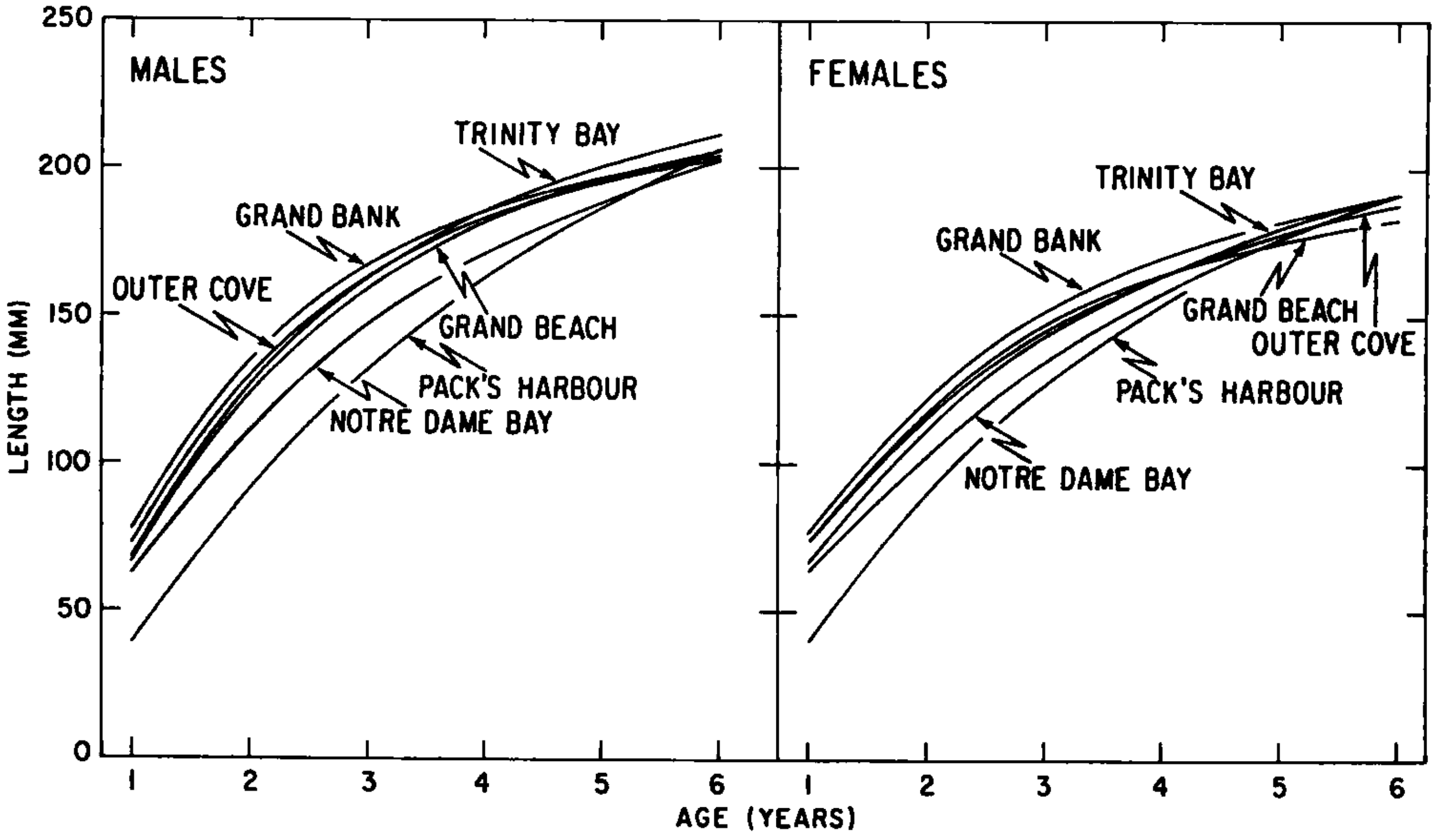

Fig. 8. Comparison of growth curves of capelin from the various areas mentioned in the text.

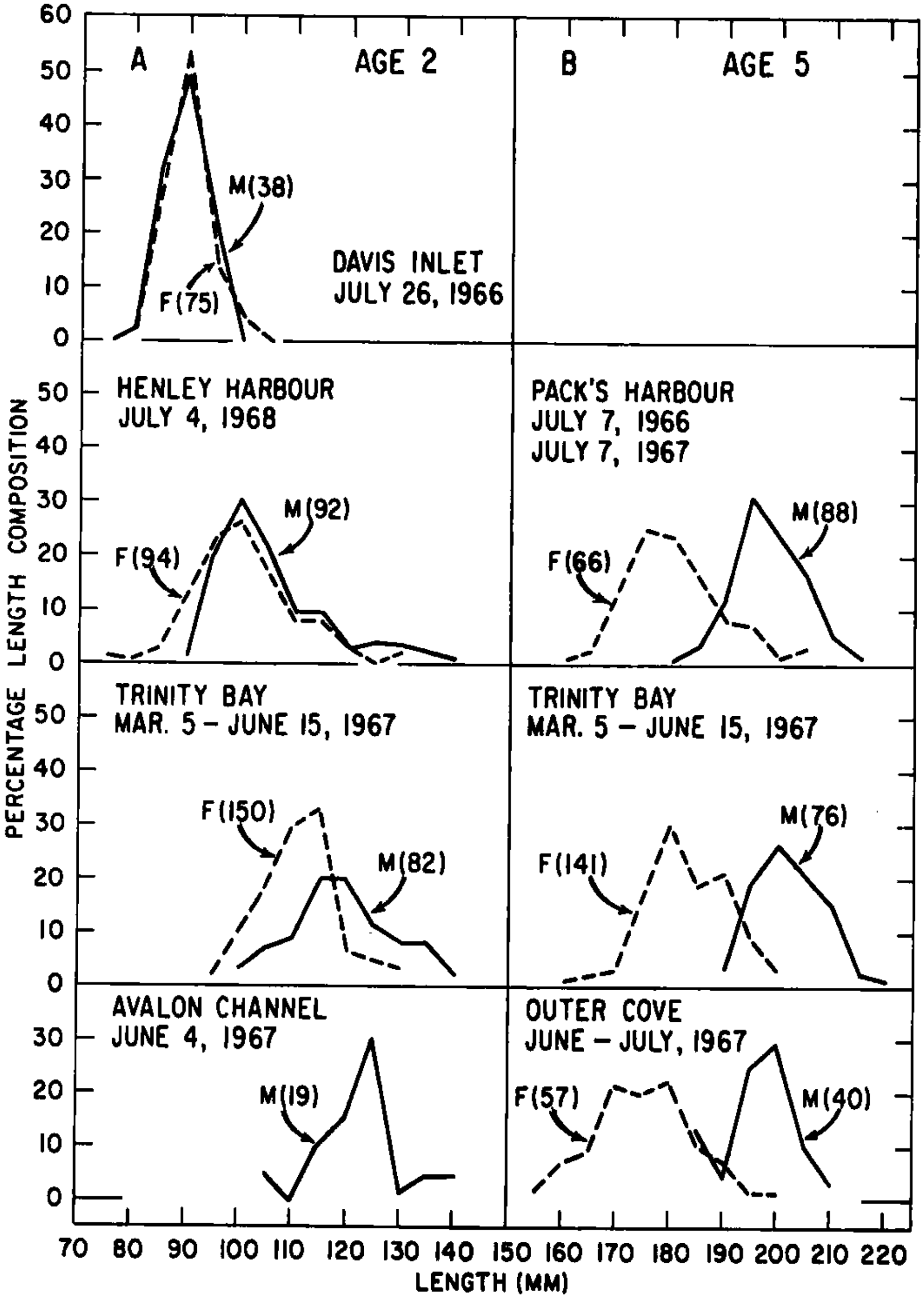

Fig. 9. Length frequency curves of immature 2-year-old (A) and mature 5-year-old (B) capelin from different areas in the Northwest Atlantic.