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Some biological aspects and population parameters of Grand Bank capelin

by

G. H. Winters and J. S. Campbell
Department of Environment
Fisheries & Marine Service
St. John's, Newfoundland.

Introduction

Although the inshore spawning of capelin continues at increasing depths to at least 35-60 m. near the Newfoundland coast (Templeman, 1948) it was not until 1950 that the presence of demersal spawning populations of capelin was observed on the southeast shoal of Grand Bank (Pitt, 1958a). Since that time only a limited amount of information has been published on the ecology and biological characteristics of offshore capelin from Grand Bank. Pitt (1958a, 1958b) has provided data on age and size composition, meristics and spawning conditions; Winters (1971, MS 1974) has provided information on fecundity and growth rates; and a variety of authors (Kovalyov and Kudrin, MS 1973; Kovalyov, MS 1972; Templeman, 1967; Dragesund and Monstad, MS 1972; Campbell and Winters, 1973) have provided information on general distribution and migration patterns. Very little knowledge, however, is available on such important parameters as maturation, recruitment and mortality rates and the effect of seasonal changes on various biological characteristics. Since 1972 an expanding fishery on spawning capelin has developed in the Southeast Shoal area with landings reaching 130,000 m. tons in 1973 and in all probability will reach the 150,000 m. ton maximum set by the Commission at the 1974 Mid-term Meeting. The need for increased biological data is therefore especially critical particularly as the Assessments Subcommittee has stipulated that further increases in recommended catch levels should be accompanied by appropriate support data justifying the increase in biological yield.

Since the late 1950's the Newfoundland Biological Station has collected, both directly and incidentally, a large amount of information on various aspects of the biology and ecology of Grand Bank capelin. These data have been collated and examined by the authors; this report presents the analyses and interpretations of such data.

Materials and Methods

The data used in this paper were obtained from random samples of capelin collected mainly during the pre-spawning and spawning seasons from 1967-73 although some data were available for nearly all seasons and as far back as 1959. Prior to 1972 most of the sample collections were obtained from catches of capelin 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. During 1972 and 1973 samples were derived mainly from commercial catches of Canadian trawlers using a Diamond VII mid-water trawl with a codend liner of 15 mm.

Lengths used are total lengths (in millimetres) measured 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). To adjust for shrinkage during preservation total lengths were multiplied by 1.03 for frozen specimens (Winters, MS 1974) and by 1.05 for specimens preserved in 95% alcohol (Winters, 1966).

Ages were determined from the lateral convex face of the otoliths and were recorded as age-groups with an arbitrary birthdate of January 1. The stage of maturity was determined by gross examination of the gonads according to the following scale: 0 = immature, 1 = maturing (pre-spawning), 2 = ripe, 3 = partly spent, 4 = spent, 5 = recovering spent. The degree of fullness of stomachs was estimated on a five-point scale according to Winters (1970) as were the stages of spawning ridge development.

Results

Length and age composition

Per mille age composition data of pre-spawning capelin from Grand Bank for the period 1967-73 (Table 1) reveal that the mature fish are dominated by 3 and 4 year-olds with only minor contributions from younger and older age-groups, particularly in the males. This suggests that 2-year-olds are mainly immature and that spawning mortality is substantial at least for 4-year-olds although perhaps not as heavy for females which are represented at age-group 5 in significant quantities in certain years.

During the period under consideration two year-classes, 1964 and 1968, dominated the mature fish for two years in succession indicating strong recruitment from those year-classes The 1966 year-class failed to be dominant in either year and appears to have been weak. Mature males are on the average about 15 mm larger than mature females with the disparity appearing to decline with age. Mean lengths at age suggest that there are considerable annual variations in growth in both sexes with the variations being consistent in direction between sexes. To assess the possible role of temperature in these annual growth variations mean lengths of mature 3 and 4-year-old capelin have been plotted against mean deviations of bottom (80 m) temperature on the northeast slope of Grand Bank during the two years previous to the sampling year from the long-term (1950-70) mean (Fig. 1). There are consistent positive correlations between temperature and growth for each age-group of each sex thus suggesting that the length achieved by any age-group is at least partly controlled by temperature conditions during the previous two years. If this is so then the fluctuations in the relative abundance of 3 and 4-year-olds in the mature fish may be interpreted as reflecting growth-induced variations in maturation rate rather than variations in survival rate. If variation in the maturation rate of year-classes is the main determinant one would expect a positive correlation between the percentage contribution of a year-class to the mature fish at age 3 and the size of that year-class at age 3; similarly one would expect a negative correlation between the same two variables at age 4, i.e. year-classes characterized by fast-growth mature mainly at age 3 whereas slow growing year-classes mature in larger proportion at age 4. To test this hypothesis the data given in Table 1 were subjected to regression analyses and linear correlation coefficients were calculated (Fig. 2). In both males and females consistent positive values of r were obtained for 3-year-olds and consistent negative values of r were obtained for 4-year-olds. This suggests rather strongly that the age-composition of spawning schools of capelin is determined more by maturation rate than by the contribution of repeat-spawners.

Length-weight and age-weight relationships

Analyses of length-weight data of pre-spawning capelin (Fig. 3) for the period 1967-73 indicate that males are heavier at length than females with both sexes increasing in weight with length at a faster rate than would be expected from the cube law. The disparity in weight at length between the sexes increases with length from just less than 3% at 150 mm to about 11% at 210 mm. Analyses of length-weight parameters for individual years from 1967-73 (Table 2) indicates substantial variation in body condition of pre-spawning capelin with regression coefficients ranging from 2.79 to 3.73 in the males and from 2.95 to 3.57 in females. This annual variation in body condition is also exhibited in weight at age data (Table 3). Whereas the disparity between sexes in terms of length at age tends to decline with age the weight differences increase with age.

Sex ratios

Sex composition of mature pre-spawning capelin from Grand Bank during the period 1967-73 is shown in Table 4. Males tended to dominate the mature fish from 1967-69 whereas females have dominated since then. There is also a general trend of declining importance of males with age perhaps reflecting a greater spawning survival of females at the older ages. For the period 1967-73 as a whole the sex ratio was slightly in favour of males and this agrees with data presented by Winters (1970) for inshore capelin.

Feeding cycle

Analysis of the degree of fullness of stomachs of maturing capelin collected during the over-wintering period in February (Fig. 4) reveals that at this time feeding intensity is very low. By early May, however, nearly 90% of the stomachs examined contained food thus indicating that feeding had resumed. Feeding intensity continued at a high level throughout May but diminished considerably in early June when nearly 60% of the stomachs examined were empty. The feeding level was further diminished during the spawning season in late June to mid-July when over 80% of the stomachs did not contain food. This decreased to about 55% in late July suggesting that feeding was being resumed in those fish which had completed spawning. Stomachs examined in September and October exhibited a high level of feeding intensity. However, by November feeding appeared to have ceased suggesting that the over-wintering period had begun. The feeding cycle of Grand Bank capelin is thus characterized by two non-feeding periods - the overwintering period lasting from November to perhaps March or April and the spawning period lasting for a period of 4-6 weeks. A similar seasonal feeding cycle was observed by Winters (1970) for coastal capelin.

Biological changes in capelin during the spawning season

1. Length and age composition

Comparison of the length and age composition of mature Grand Bank capelin from the pre-spawning to the spawning condition (Fig. 5) indicates that in 1972 there was very little change in either the length or age characteristics of the males. Amongst the females, however, there was a clear trend of increasing contributions from younger fish as the spawning season progressed suggesting that the older females spawned first. Similar observations were made by Templeman (1948) for beach-spawning capelin.

Samples obtained during 1973 (Fig. 6) confirm the relative stability of the age and length characteristics of males during the spawning season. However, there is much less of a shift towards the younger age-groups among the females although the length compositions do shift significantly towards the smaller fish as the spawning season advanced, suggesting that there was also a change in the mean lengths of the individual age-groups. To evaluate this possibility, mean lengths of mature fish of age-groups 3-5 were plotted against the relative time during the spawning season in 1972 and 1973 (Fig. 7). There is very little change in the mean length at age of males whereas females exhibit a pattern of decreasing length at age for both years and for all mature age-groups. This indicates that amongst the females the faster-growing fish of a year-class spawn first and are subsequently replaced by slow-growing, later-maturing individuals.

2. Length-weight and weight-age

There is a consistent decline in weight at length of female capelin from the pre-spawning to the spawning condition (Fig. 8). This decrease is particularly substantial during the spawning season from June to July and reflects not only the general decline in body condition due to maturation (Winters, 1970) but also the loss in body weight associated with egg discharge. Males tend to be somewhat different than females and exhibit an increase in weight at length from April-May to June followed by a considerable decrease in weight at length from June to July. Weight at age data (Table 5) reveal a similar trend in body condition.

The increase in body condition of males from April-May to June seems anomalous in that no differences were observed in feeding patterns of males and females and also Winters (1970) has shown that for both sexes of coastal capelin, which have a similar feeding pattern, there is a continuous decrease in weight at length from the pre-spawning to the ripe condition. Fat content data followed a similar pattern. It is therefore possible that the increase in body condition of male capelin from April-May to June is not normal or reflects some bias in sample estimates, perhaps due to small sample size.

3. Sex ratios

Sex compositions of Canadian commercial catches of capelin on the Southeast Shoal of Grand Bank during 1972 and 1973 are shown in Fig. 9. In both years females were dominant in June, particularly the last half of June whereas males dominated the catches throughout July and early

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August. The sex composition of Norwegian commercial capelin catches on the Southeast Shoal in 1973 was, however, opposite to Canadian data and indicate a significant predominance of females (Dommasnes et al, 1974). The differing results are possibly due to the segregation and relative distribution of the sexes in relation to the type of gear used. The sexes are normally separated during the spawning season (Templeman, 1948) and on the Southeast Shoal this spatial separation occurs vertically with the males being normally located near the bottom spawning beds and the females being concentrated pelagically. It is not known whether the Norwegians were intentionally sex-selective in their fishing operations but the much larger mouth openings of Norwegian mid-water trawls compared to the Canadian trawls (29 m. versus 12-16 m) would have undoubtedly contributed to the dominance of females in the Norwegian catches.

4. Secondary sexual characteristics

The maturation process in capelin is associated with the development of secondary sexual characteristics which accentuates sexual demorphism and allows easy sex differentiation in spawning fish (Templeman, 1948; Winters, 1970). Spawning ridges begin to appear on the males from Grand Bank in early May (Fig. 10) and develop rapidly to reach the stage of full development at the beginning of the spawning season in June. During the same period and particularly in June the eggs of the females increase greatly in volume (Fig. 10) resulting in a plump appearance which together with the spawning ridges of males facilitates sex separation. The testes of the males do not increase in size from the pre-spawning to the ripe condition and remain fairly constant in size throughout the spawning season.

5. Maturity composition

Maturity composition data (Fig. 11) reveal that during 1972 and 1973 partly spent fish predominated amongst the males throughout the spawning season with very few fish in the ripening stage (stage 1). The high proportion of partly-spent males on the spawning grounds agrees with observations by Templeman (1948) that the males remain at the spawning area for prolonged periods of time and individually service large numbers of females. It also agrees with the lack of a trend in size and age composition of male capelin as the spawning season progresses.

Female capelin from the Southeast Shoal tend to fall into two main categories - ripe and spent with very few partly spent fish suggesting that egg expression is completed in one mating act. Consequently it appears that new schools of females are continuously recruiting to the spawning area and accounts for the decrease in mean age and length demonstrated in Fig. 7.

6. Nematode infection

Capelin are parasitized by larval nematodes at least one of which is Contracaecum sp. (Templeman, 1948). Both the incidence (percentage infection) and the intensity (mean number per fish) of nematode occurrence in Grand Bank capelin are at a low level during the winter period (Fig. 12) but increase dramatically as feeding resumes in April and May. The infection rate remains at a high level until early June when both the incidence and intensity drop substantially. This is probably due to the extrusion of the nematodes along with the genital products during the spawning season. There appears to be a slight increase in the nematode infection rate after spawning but not to the level achieved just prior to the spawning period.

Size and age at maturity

Because of the difficulty of obtaining significant numbers of immature and mature capelin in the same set, particularly during the pre-spawning and spawning seasons when most of the sample collections were made, per mille length compositions were calculated for each sex for each group and compared to provide relative percentage mature at length. Maturity curves were then fitted for each sex by probit analysis as described by Fleming (1960) (Fig. 13). Females mature at a smaller size than males with the size at 50% maturity occurring at 149 mm compared to 165 mm for males. The smallest mature female measured 120 mm and the smallest male 135 mm.

Mean per mille age compositions of mature and immature capelin for the periods 1967-68, 1972-73 are compared in Table 6. The maturation rates of males and females are very similar with less than 2% of age-group 2 fish being mature, increasing to about 42% at age-group 3, 92% at age-group 4 and 100% for both sexes at age-group 5.

A further indication of the magnitude of spawning survival can be obtained by comparing the accumulative mean age composition of mature fish given in Table 1 with the percentage mature at age, i.e. if spawning survival were negligible then the two sets of data should agree. This has been done in the last two columns of Table 6. The very good agreements between the two sets of data suggests that spawning survival is not a significant contributor to the age composition of mature fish and supports the indication of high spawning mortality demonstrated in Fig. 2.

Estimates of total mortality

Evidence presented in previous sections of this paper have indicated that repeat-spawners do not contribute significantly to the spawning population. If this can be assumed true and the sampling gear is non-selective, then in any particular year the maturation rate will be equivalent to the recruitment rate, since the Southeast Shoal fishery is based completely on mature capelin. Thus if one assumes also that the mean age compositions and maturation rates given in Tables 1 and 6 respectively are representative of Grand Bank capelin during the period under consideration (1967-73) then the mean relative number of any age-group present during this period (N_T) can be calculated as follows:

$$N_T = \frac{N_M}{R}$$

where N_M = relative number of mature fish in an age-group

R = recruitment rate (= maturation rate) applicable to that age-group

The mean age compositions of mature fish for the period 1967-73 given in Table 1 have been adjusted in this manner and plotted as a simple catch curve (Fig. 14). Average total mortality estimates are very high for both sexes from age-group 3 onwards, the estimate for the males being considerably higher than that for the females. Mortality estimates have also been calculated for the various age-groups as follows:

	Males		Females	
Age-group	Z	e^{-Z}	Z	e^{-Z}
3-4	.71	.49	.75	.47
4-5	2.62	.07	1.44	.24
5-6	2.97	.05	2.01	.13

Mortality estimates increase substantially with age in both sexes and with the exception of age-group 3, males suffer much higher mortalities than females. From a comparison of age and length compositions of post-spawning and pre-spawning capelin from Grand Bank Winters (MS 1974) also concluded that spawning survival favoured the younger and smaller fish.

The mortality estimates given above reflect not only the spawning mortality associated with mature fish during spawning (S) but also all other causes of natural mortality (M), i.e. for any age-group containing mature fish Z = M + pS where p = proportion mature at age. If, for instance, M is assumed to be 0.20 for age-group 3 females this implies a spawning mortality of 1.44 or a survival rate of 24%. Thus it can be seen that even in the younger age-groups survival of the spawning cohort is low, probably being less than 20% for the spawning population as a whole.

Yield per recruit

Yield per recruit curves have been calculated for males and females separately using the age-specific mortality rates given above. For this purpose age-group and fishery year have been defined as extending from the beginning of the post-spawning season in one year to the end of the spawning season in the subsequent year and spawning mortality is assumed to occur at the end of the spawning season, i.e. at the end of the fishery and the beginning of the next fishery year. Thus for example the spawning mortality of 3-year-olds is applied as loss in yield to that year-class as 4-year-olds. Natural mortality is assumed to be 0.20 for age-groups 1 and 2 and a range of 0.20-0.30 has been assumed for 3-year-olds. Mean age-specific weights for June and July given in Table 5 have been used and recruitment rates have been considered equivalent to the mean maturation rates given as Table 6.

The yield per recruit curves for both sexes are flat-topped (Fig. 15) with a maximum yield per recruit occurring at a fishing mortality rate greater than 3.0. Males have a much larger yield per recruit than females which is to be expected from their much greater weight at age. For most Northwest Atlantic fish stocks the optimum fishing mortality rate as defined by Gulland and Baerema (1973) and calculated by the graphical method, approximates 90% of the maximum yield per recruit. Estimated in this manner, $F_{.1}$ values range from 1.8-1.9 for both sexes for values of M = 0.20 and 0.30 respectively.

The above fishing mortality rates apply to the fully recruited age-groups of capelin which for the Southeast Shoal fishery represents age-group 5 and older. These age-groups, however, comprise less than 10% of the exploited stock and the more pertinent mortality rates are those for age-groups 3 and 4 which can be obtained by simple application of partial recruitment rates.

Discussion and Conclusions

Age composition data of mature capelin from Grand Bank for the period 1948-50 (Pitt, 1958a) show that age-group 3 dominated the spawning schools with age-group 4 comprising less than 4% and age-group 5 and older being absent altogether. This is in contrast to age-composition data presented in this paper which reveal that during the period 1967-73 4-year-olds were more abundant than 3-year-olds in the mature fish and 5 and 6-year-olds were also present in significant quantities. Assuming that length at maturity has remained constant and in view of the implicit relationship between growth and age at maturity demonstrated in Fig. 2, these differences in age composition data suggest that Grand Bank capelin were faster growing and matured at an earlier age during the late 1940's than in recent years. Age-specific total lengths (adjusted, where necessary, for shrinkage due to preservation) of mature capelin from Grand Bank for the periods 1948-50, and 1967-73 and of mature inshore capelin from the Avalon Peninsula of Newfoundland during the early 1940's (Templeman, 1948) are shown below:

		Total length (mm)	
Area	Sex	Age-group 3	Age-group 4
Grand Bank, 1948-50	M	187	
	F	162	
Grand Bank, 1967-73	M	179	187
	F	163	172
Avalon Peninsula, 1940-41	M	185	191
	F	164	178

Grand Bank males were significantly larger at age-group 3 during the late 1940's than in recent years although no differences are evident in age-group 3 females. Assuming that the similarity in growth between inshore capelin from the Avalon area and Grand Bank capelin (Winters, MS 1974) also applied during the early 1940's, then Templeman's data also suggest that growth rates of capelin were higher during the 1940's than during the years 1967-73.

Significant correlations between growth rates and water temperatures have already been demonstrated for Grand Bank capelin (Fig. 1). Since the early 1950's there has been a consistent decline in water temperature in the Northwest Atlantic area (Rodewald, 1972; Lauzier, 1967; Chase, 1967) with the 1966-70 pentade being 0.43°C colder than the 1951-55 pentade. This trend of climatic deterioration has continued and intensified in the early 1970's. It is therefore quite probable that the retardation of growth and change in age composition of Grand Bank capelin since the late 1940's has been due to the effects of lower water temperatures. In this regard it is interesting to note that in 1972 and 1973 both of which were characterized by very cold temperature conditions, 4-year-olds predominated amongst the mature fish.

The high spawning mortality estimated for Grand Bank capelin implies that both maximum and optimum yield per recruit of a cohort can only be achieved by generating extremely large amounts of fishing effort which, if applied to mature fish, will have only a minimal effect on subsequent yields from that year-class. Maintenance of appropriate yield per recruit conditions should not therefore be a prime consideration in management actions directed towards the Southeast Shoal fishery but rather the more important consideration should be the assurance of adequate spawn deposition. In this respect data presented above reveal that spent and partially spent capelin make up a significant portion of the commercial fishery on the Southeast Shoal so that the effect of fishery removals on the amount of egg deposition is somewhat ameliorated. Whether or not an unregulated fishery would reduce egg deposition levels to the point of inadequate recruitment can only be speculated. However, there are two aspects of the life history of Grand Bank capelin which may be useful to management aims. The first point is that male capelin remain on the spawning grounds for prolonged periods of time and spawn repeatedly during the spawning season. Consequently the removal of one male has much less effect on the amount of viable spawn than one female. Secondly there is usually a depth segregation of males and females on the spawning grounds with the females being located at mid-depths and the males near bottom. Thus by using an appropriate type of gear (such as a bottom trawl or a mid-water trawl with a small mouth opening) and/or fishing strategy (concentrating fishing effort during those times of the day when the sexes are segregated) the spawning population can be fished selectively so that the greater proportion of the fishing effort is directed towards the males. In addition such measures will act to decrease the relative proportion of ripe to spent females in the catch.

A variety of other qualitative conservation measures could also be applied to ensure adequate recruitment potential such as periodic breaks in fishing, closed areas or a combination of both. A more effective method of regulation would be of course to establish total allowable catch levels in relation to annual estimates of spawning stock. The above measures would then be of greatest value as safeguards in years when estimates of spawning stock size are not available or are too high in relation to recommended catch levels. In all cases, however, more refined information is required on the characteristics of spawning fish particularly their depth stratification in relation to sex, diurnal behaviour, conditions required for spawning, etc., as well as new data on the physical description of the spawning grounds.

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Table 1. Per mille age-composition and mean length-at-age ($\bar{T}$) of mature pre-spawning male (A) and female (B) capelin from Grand Bank.

	Age 2		Age 3		Age 4		Age 5		Age 6	
Year	°/₀₀	$\bar{T}$ (mm)	°/₀₀	$\bar{T}$ (mm)	°/₀₀	$\bar{T}$ (mm)	°/₀₀	$\bar{T}$ (mm)	°/₀₀	$\bar{T}$ (mm)
(A)										
1967	3	161	657	183	311	191	30	198	-	-
1968	5	166	464	179	509	190	21	199	-	-
1969	11	154	284	178	659	185	45	196	-	-
1970	59	172	663	181	238	187	30	200	10	200
1971	-	-	579	177	404	192	17	201	-	-
1972	-	-	382	180	605	183	13	186	-	-
1973	14	153	146	175	724	182	116	186	-	-
Mean	13	161	453	179	493	187	39	195	2	200
(B)										
1967	13	137	494	164	301	173	177	179	15	189
1968	6	143	350	162	465	172	147	184	32	190
1969	43	150	367	159	475	172	101	180	14	182
1970	28	155	468	168	275	176	193	183	37	192
1971	22	150	671	164	308	173	-	-	-	-
1972	-	-	387	164	557	172	47	185	9	191
1973	24	148	181	158	675	167	120	175	-	-
Mean	19	147	417	163	437	172	112	181	15	189

Table 2. Length-weight parameters of male and female capelin from Grand Bank for the period 1967-73 (b = regression coefficient, a = intercept).

	MALES			FEMALES		
	b	($x^{a} 10^{-6}$)	N	b	a	N
1967	3.62	.211	401	2.95	6.562	388
1968	3.59	.249	732	3.25	1.342	345
1969	3.60	.256	175	3.09	3.436	129
1970	3.20	2.280	106	3.00	6.068	119
1972	3.73	.132	159	3.57	.282	152
1973	2.79	17.423	68	3.08	3.648	80

Table 3. Age-specific weights of pre-spawning male and female capelin from Grand Bank.

	Age 2		Age 3		Age 4		Age 5		Age 6	
	M	F	M	F	M	F	M	F	M	F
1967	20	14	34	23	39	28	45	30	-	43
1968	19	11	30	20	38	24	49	30	-	31
1969	20	16	28	20	36	23	39	29	-	-
1970	-	15	34	22	44	27	58	32	-	-
1971	28	22	35	26	40	30	48	33	51	35
1972	-	-	33	24	35	27	35	33	-	-
1973	-	14	25	25	35	26	37	31	-	-
Mean	22	15	31	23	38	26	44	31	51	36

Table 4. Sex ratios (% male) by age of pre-spawning capelin from Grand Bank, 1967-73.

	1967		1968		1969		1970		1971		1972		1973		Total	
	N	%M	N	%M	N	%M	N	%M	N	%M	N	%M	N	%M	N	%M
2	6	16.7	3	66.7	8	25.0	9	66.7	2	0.0	-	-	2	50.0	30	40.0
3	456	57.9	229	76.0	96	52.1	114	58.8	83	39.8	75	45.3	24	41.7	1077	58.7
4	342	51.7	264	72.3	179	64.8	52	46.2	65	35.4	119	50.4	106	47.2	1027	57.4
5	81	14.8	31	25.8	22	36.4	23	13.0	1	0.0	5	0.0	18	44.4	181	22.1
6	6	0.0	5	0.0	2	0.0	5	20.0	-	-	1	0.0	-	-	19	5.3
Total	791	50.8	532	70.5	307	57.3	203	49.8	151	37.7	200	47.0	150	46.0	2334	54.6

Table 5. Weight at age data of mature Grand Bank capelin from the pre-spawning to the spawning condition

	2		3		4		5		6	
Males	N	$\overline{W}$	N	$\overline{W}$	N	$\overline{W}$	N	$\overline{W}$	N	$\overline{W}$
May	1	19.0	13	32.8	171	34.0	11	34.9		
June			40	34.8	105	37.6	5	38.0		
July	6	23.3	174	27.6	1040	31.6	90	33.7	5	38.4
Mean	7	22.7	227	29.2	1316	32.4	106	34.0	5	38.4
Females										
May	-	-	23	24.6	88	26.1	14	31.6	-	-
June	3	19.3	130	20.8	337	23.9	28	29.3	-	-
July	10	15.7	107	14.8	165	19.8	23	26.1	9	35.2
Mean	13	16.5	260	18.7	490	27.8	65	28.7	9	35.2

Table 6. Comparison of mean per mille age compositions of immature and mature capelin for the periods 1967-68, 1972-73. The last column represents the accumulative age composition of mature fish for the period 1967-73 (Table 1), both sexes combined.

Age -group	Males			Females			Both sexes			Accumulative mean age composition (%)
	Imm	Mat	% Mat	Imm	Mat	% Mat	Imm	Mat	% Mat	
2	415	6	1.4	423	6	1.4	838	12	1.4	1.6
3	518	412	44.3	557	353	38.8	1075	765	41.6	45.1
4	67	537	88.9	20	500	96.2	87	1037	92.2	91.6
5	-	45	100.0	-	123	100.0	-	168	100.0	99.2
6	-	-	100.0	-	18	100.0	-	18	100.0	100.0

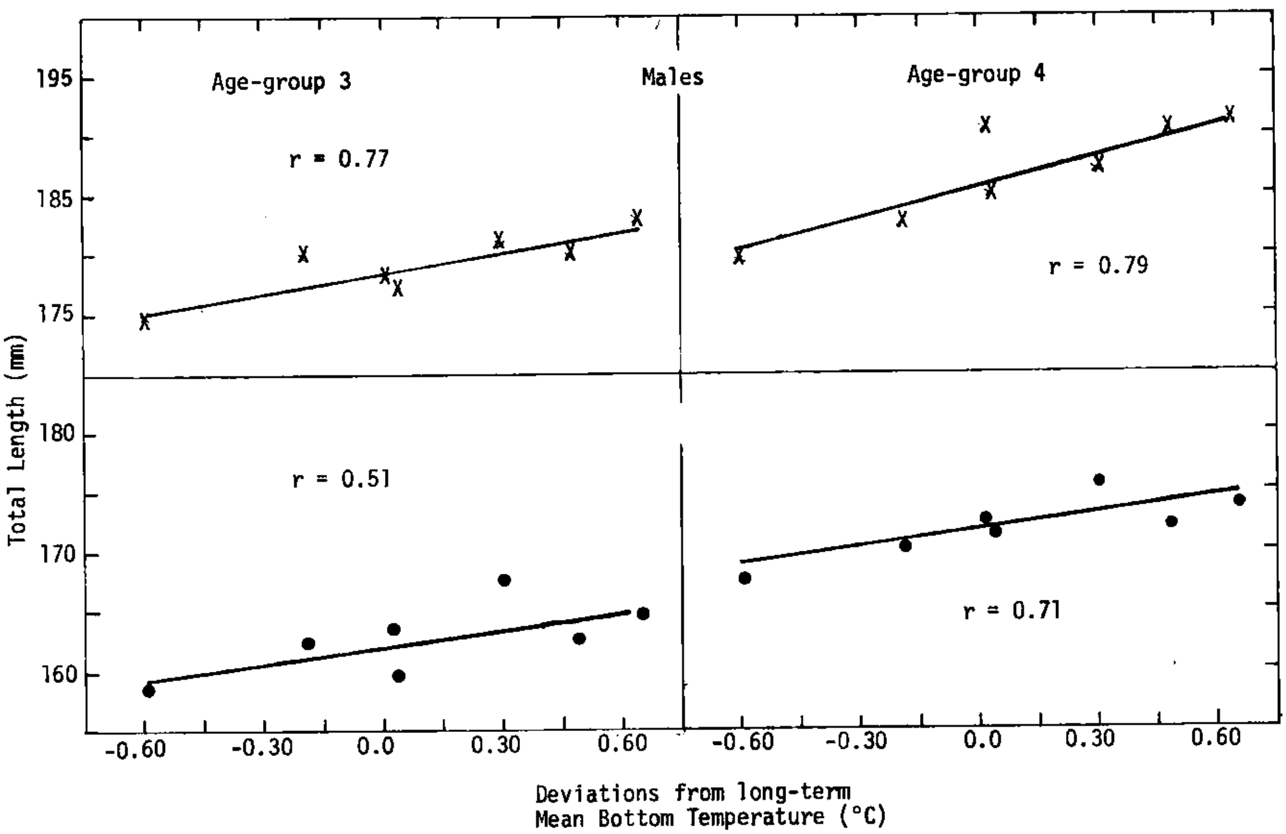

Fig. 1. Relationship between mean length of mature 3 and 4 year old capelin from Grand Bank and bottom temperature anomalies (deviations from 1950-70 mean) on the northeast slope of Grand Bank.

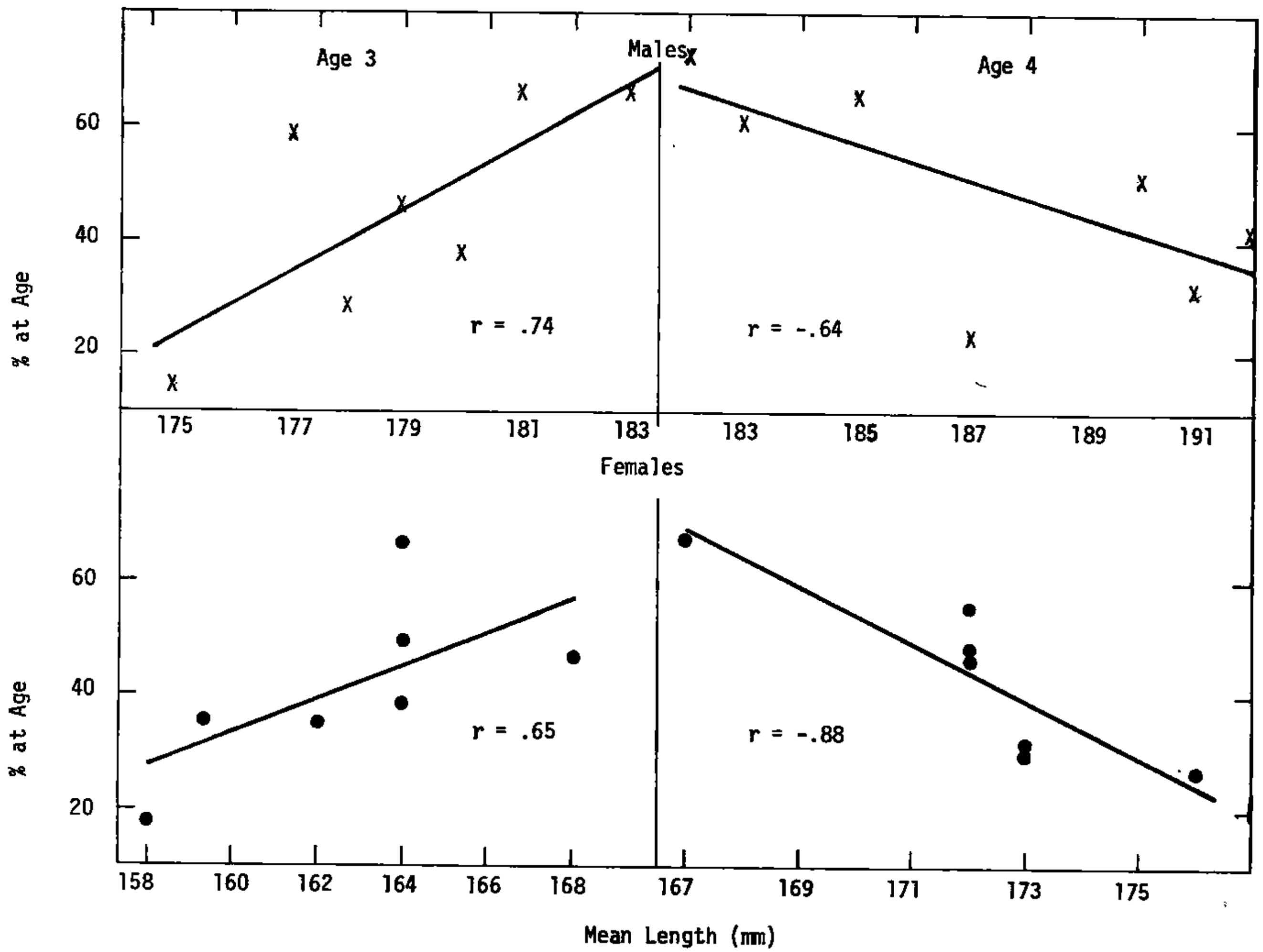

Fig. 2. Percentage contribution of 3 and 4 year old fish to the mature schools of Grand Bank capelin in relation to mean length at those ages.

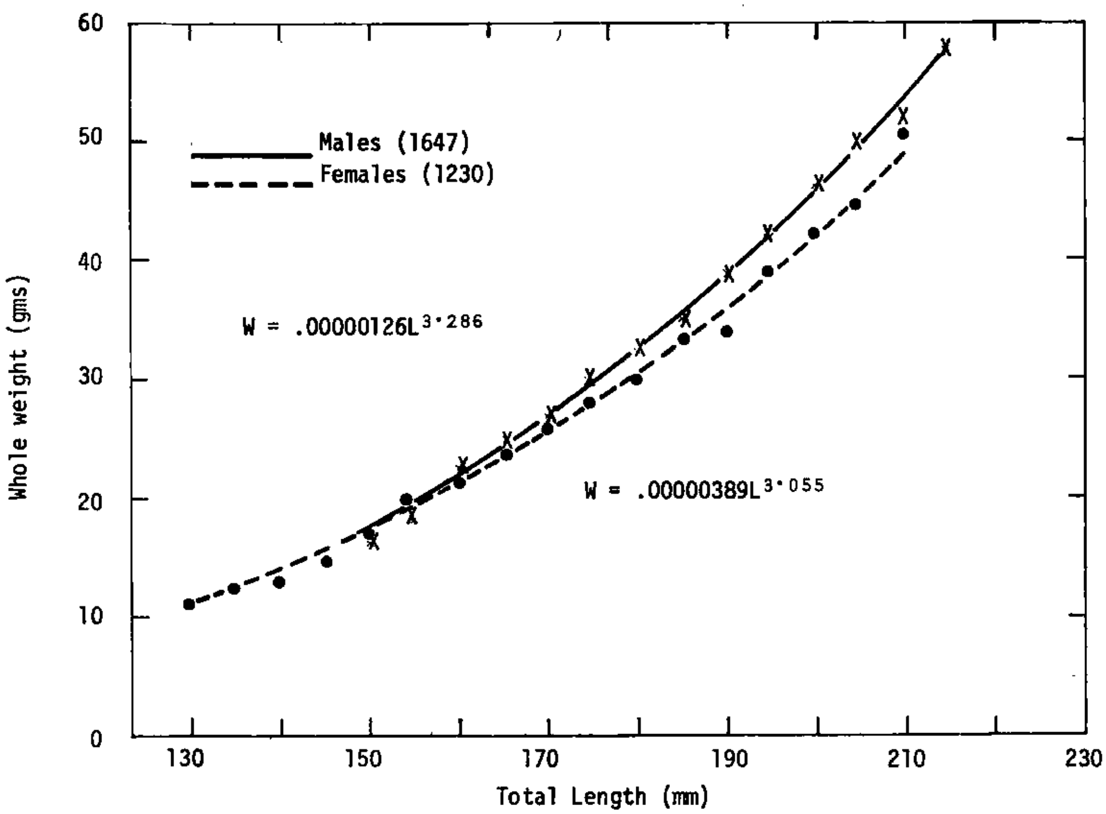

Fig. 3. Length-weight relationship of pre-spawning Grand Bank capelin for the period 1967-73.

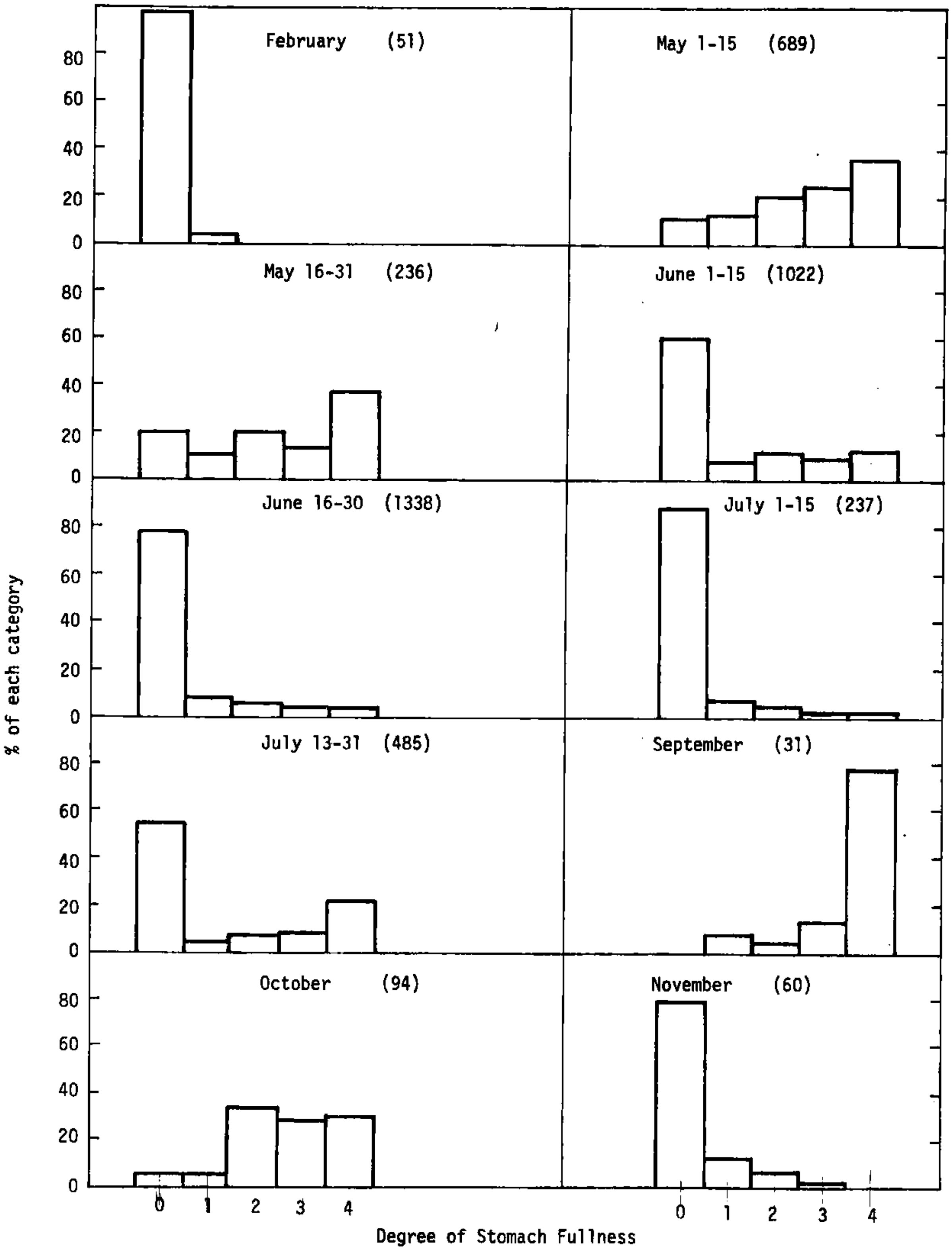

Fig. 4. SEASONAL variation in feeding levels of Grand Bank Capelin as indicated by degree of fullness of stomachs.

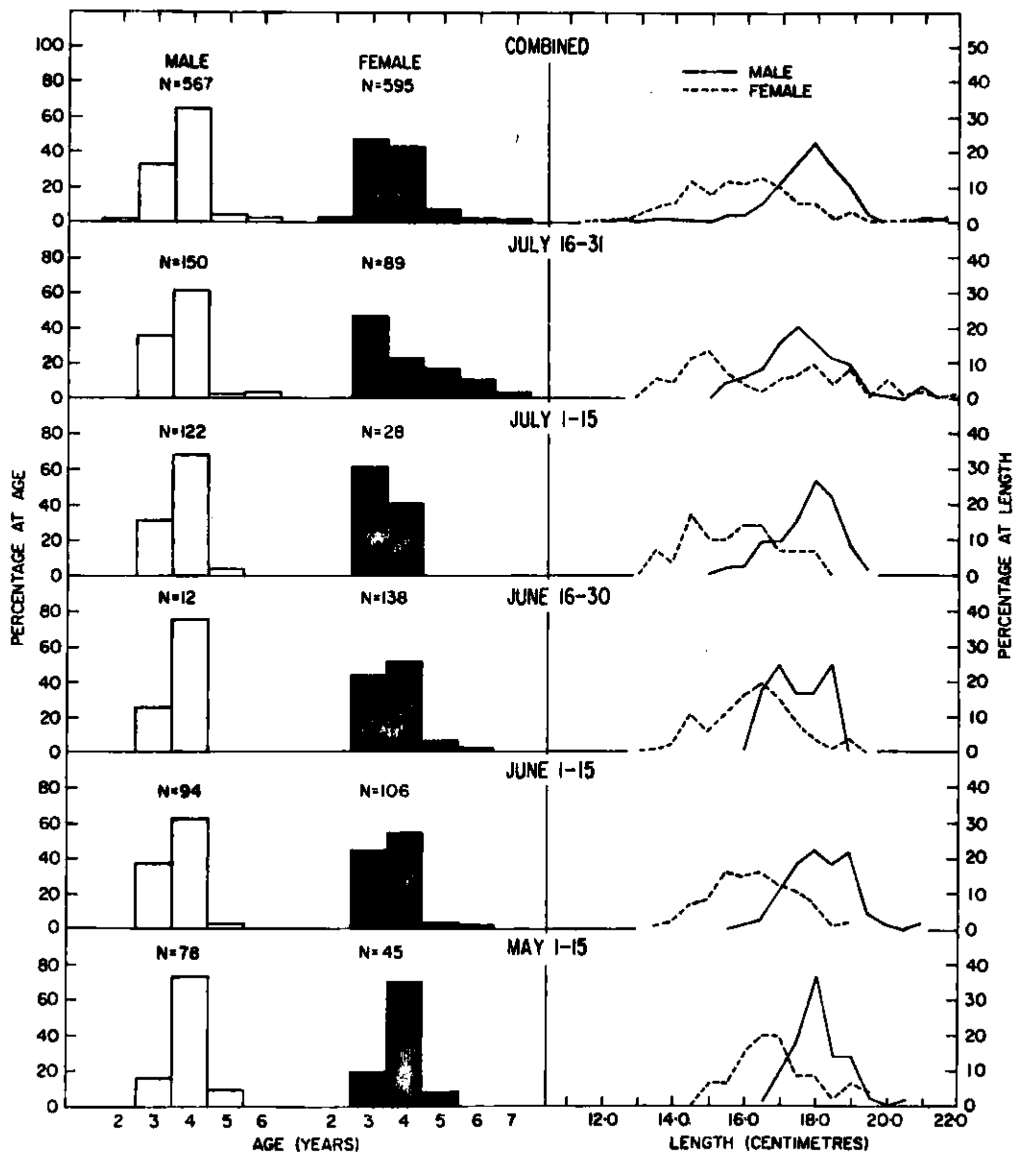

Fig. 5. Age and length composition of mature capelin from Grand Bank during 1972

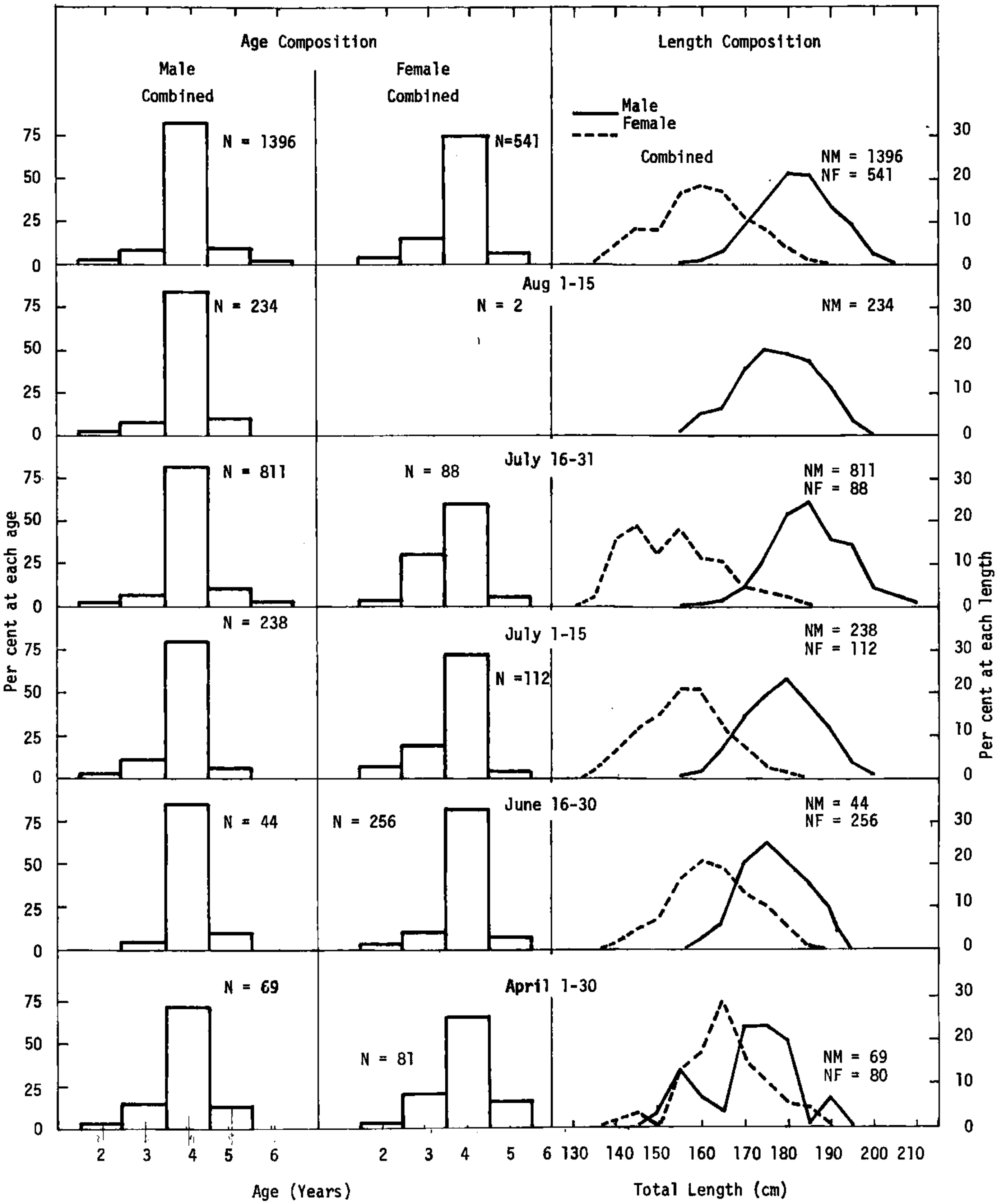

Fig. 6. Length and age composition of commercial catches of mature capelin from Grand Bank during 1973.

F 3

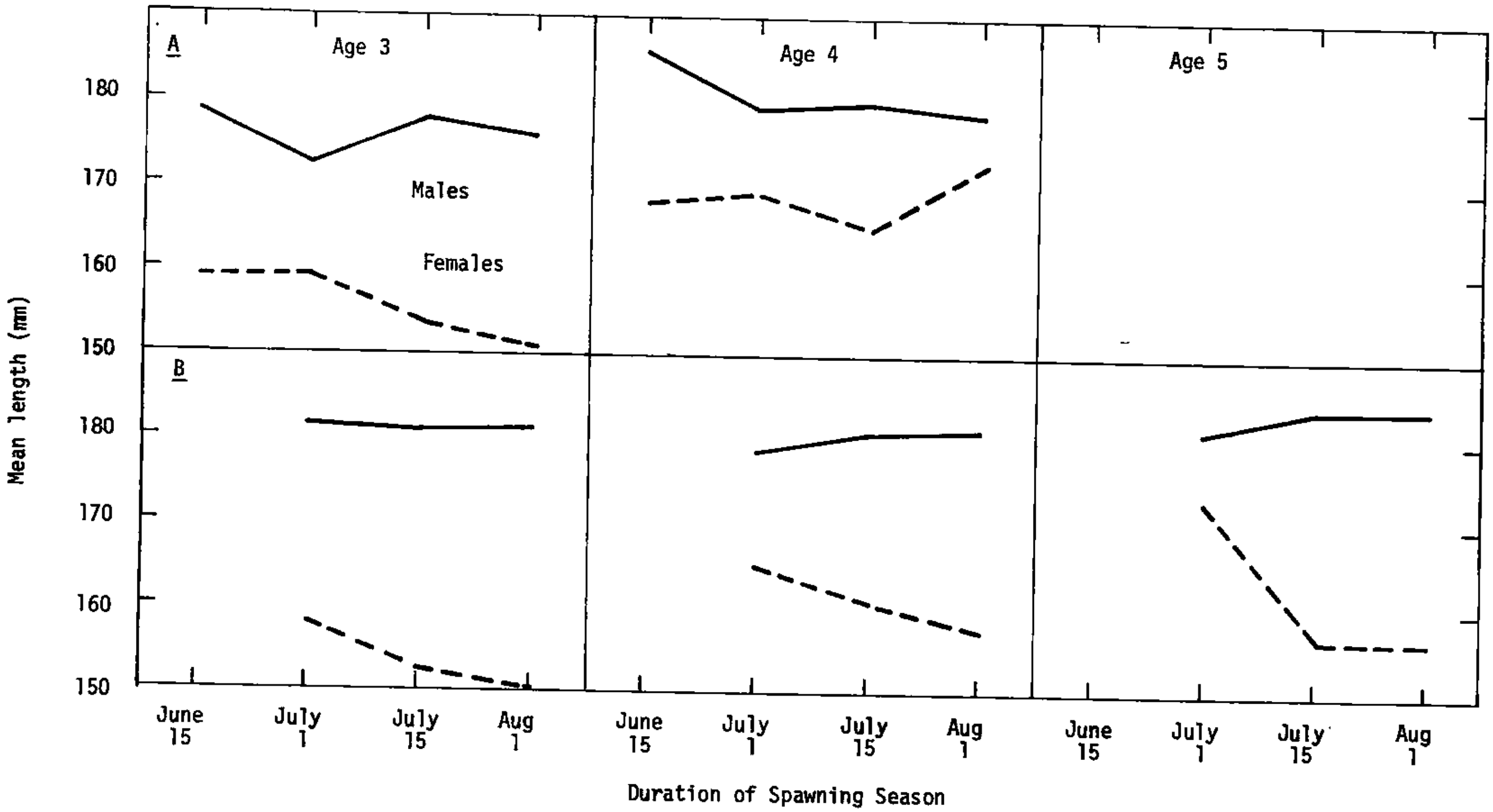

Fig. 7. Variation in mean lengths of mature 3, 4 and 5-year-old Grand Bank capelin in relation to the progression of the spawning season during 1972 (A) and 1973 (B).

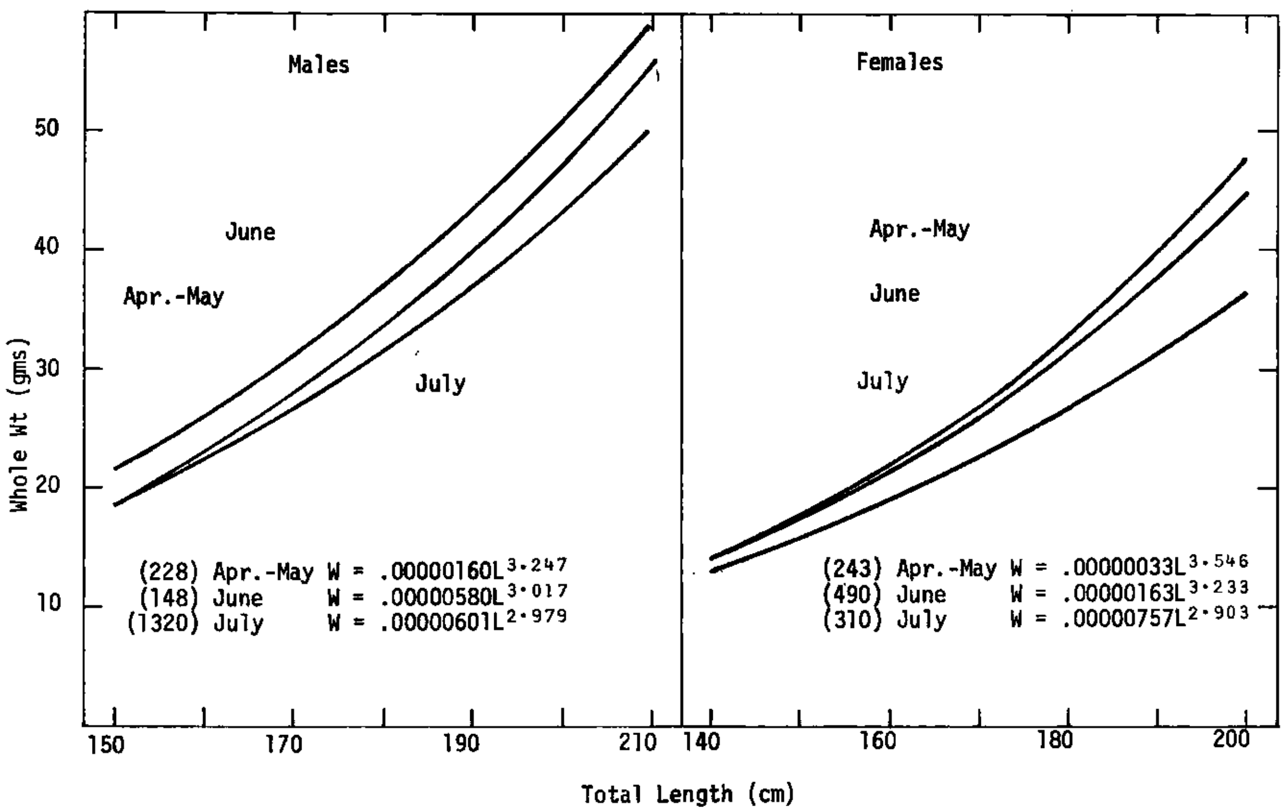

Fig. 8. Length-weight relationship of Grand Bank capelin from the pre-spawning to the spawning condition.

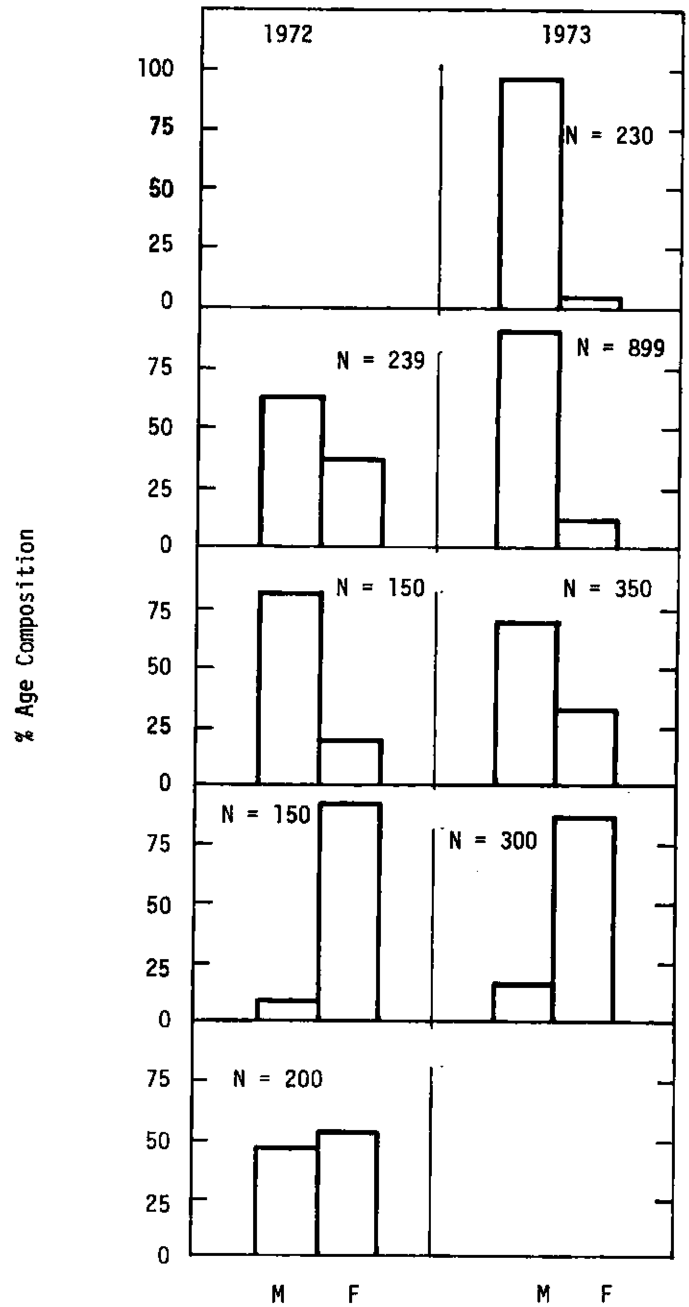

Fig. 9. Sex composition of commercial catches of capelin by Canadian vessels on the Southeast Shoal during 1972 and 1973.

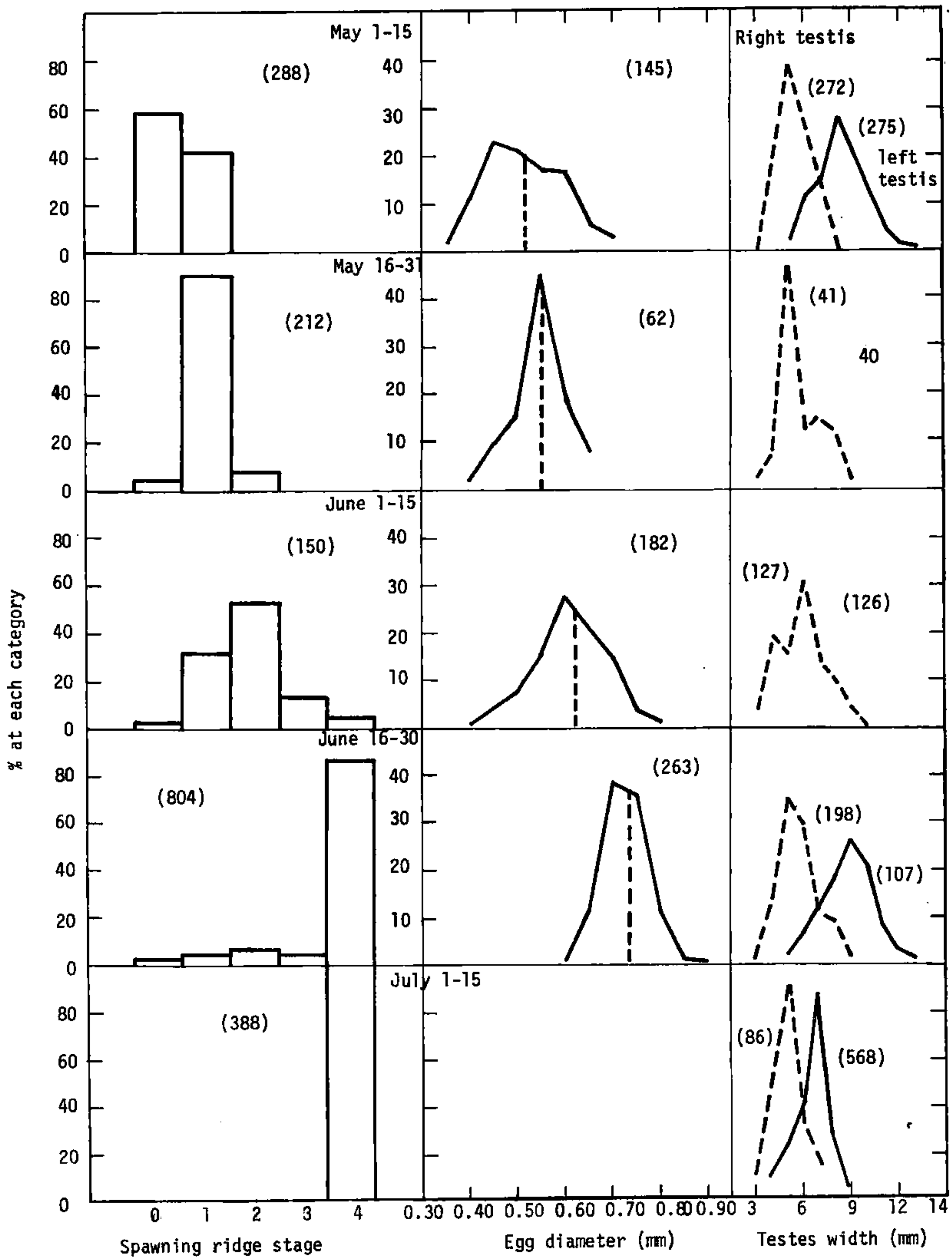

Fig. 10. Development of the spawning ridges, ovaries and testes of Grand Bank capelin from the pre-spawning to the spawning condition.

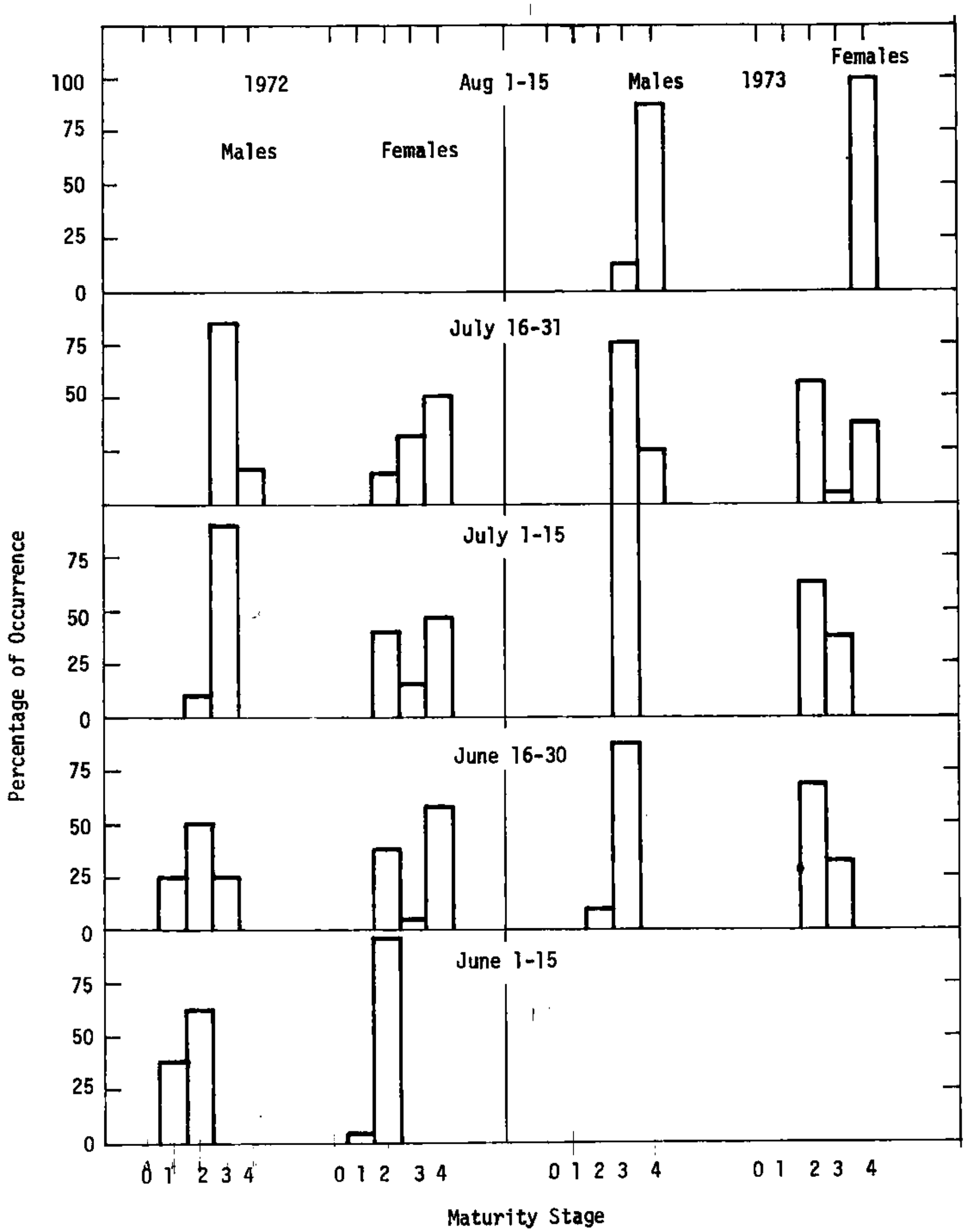

Fig. 11. Maturity composition of male and female capelin from the Southeast Shoal of Grand Bank. during 1972 and 1973.

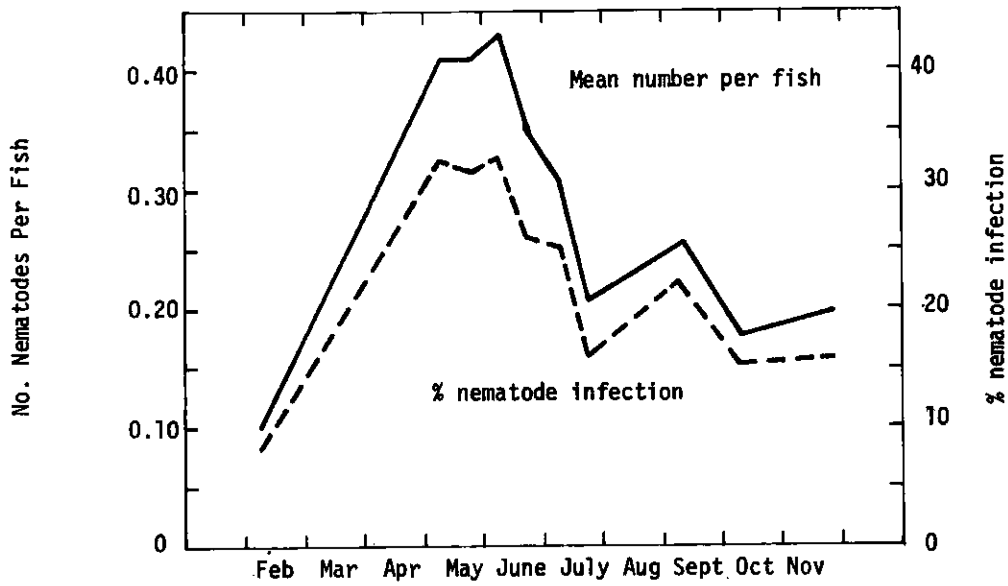

Fig. 12. Nematode occurrence in Grand Bank capelin in relation to season.

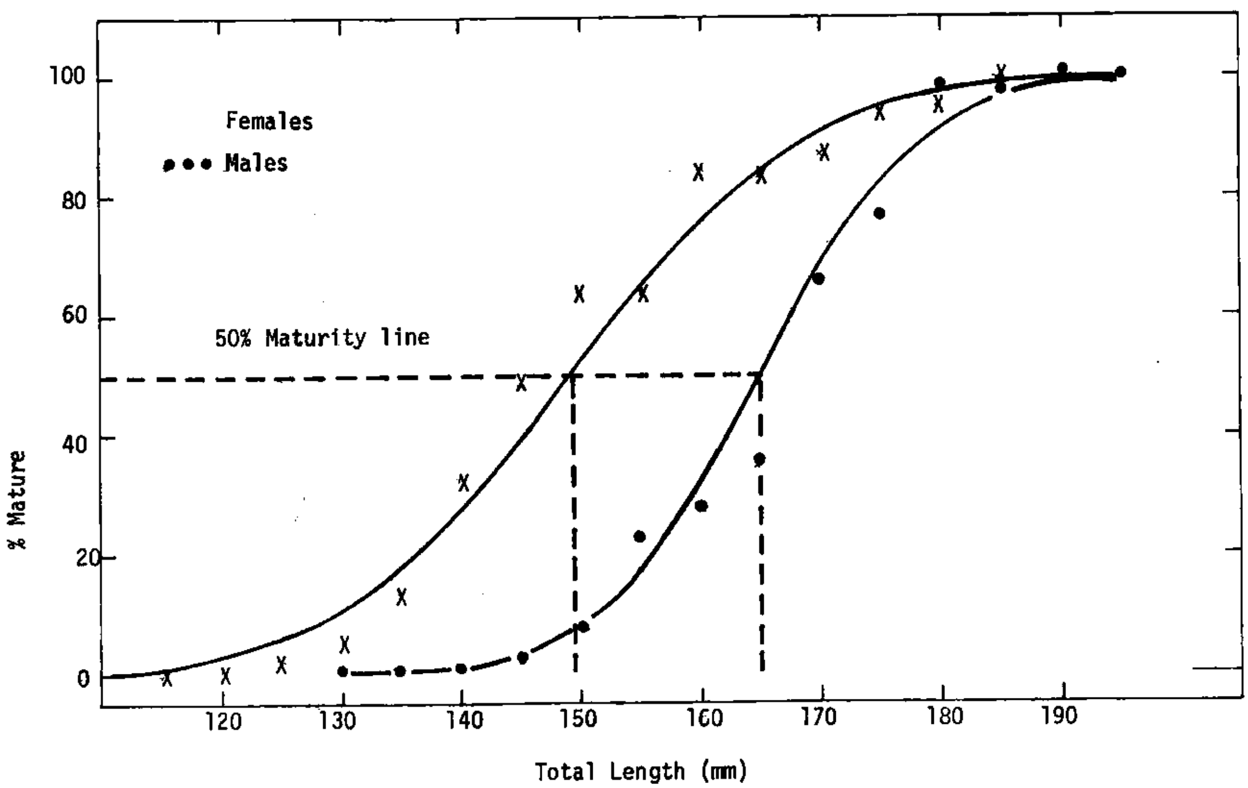

Fig. 13. Maturity ogives of male and female capelin from Grand Bank.

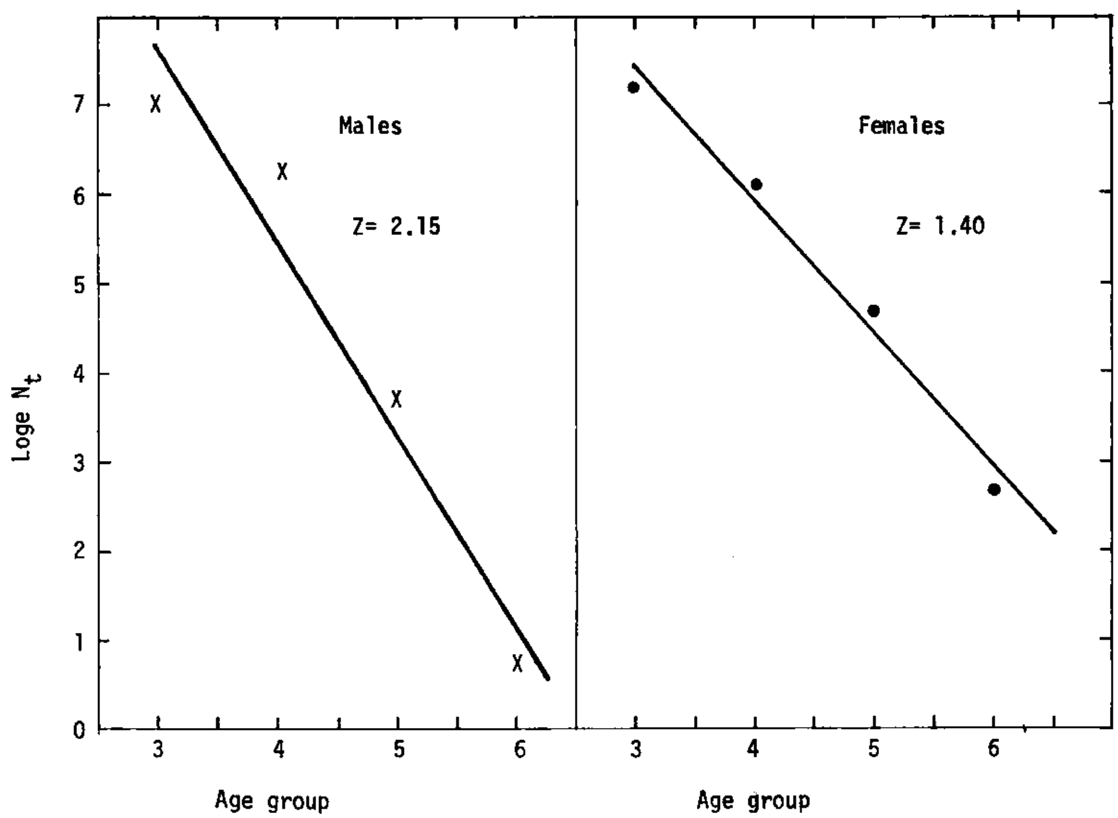

Fig. 14. SIMPLE catch curves of male and female Grand Bank capelin (see text for explanation)

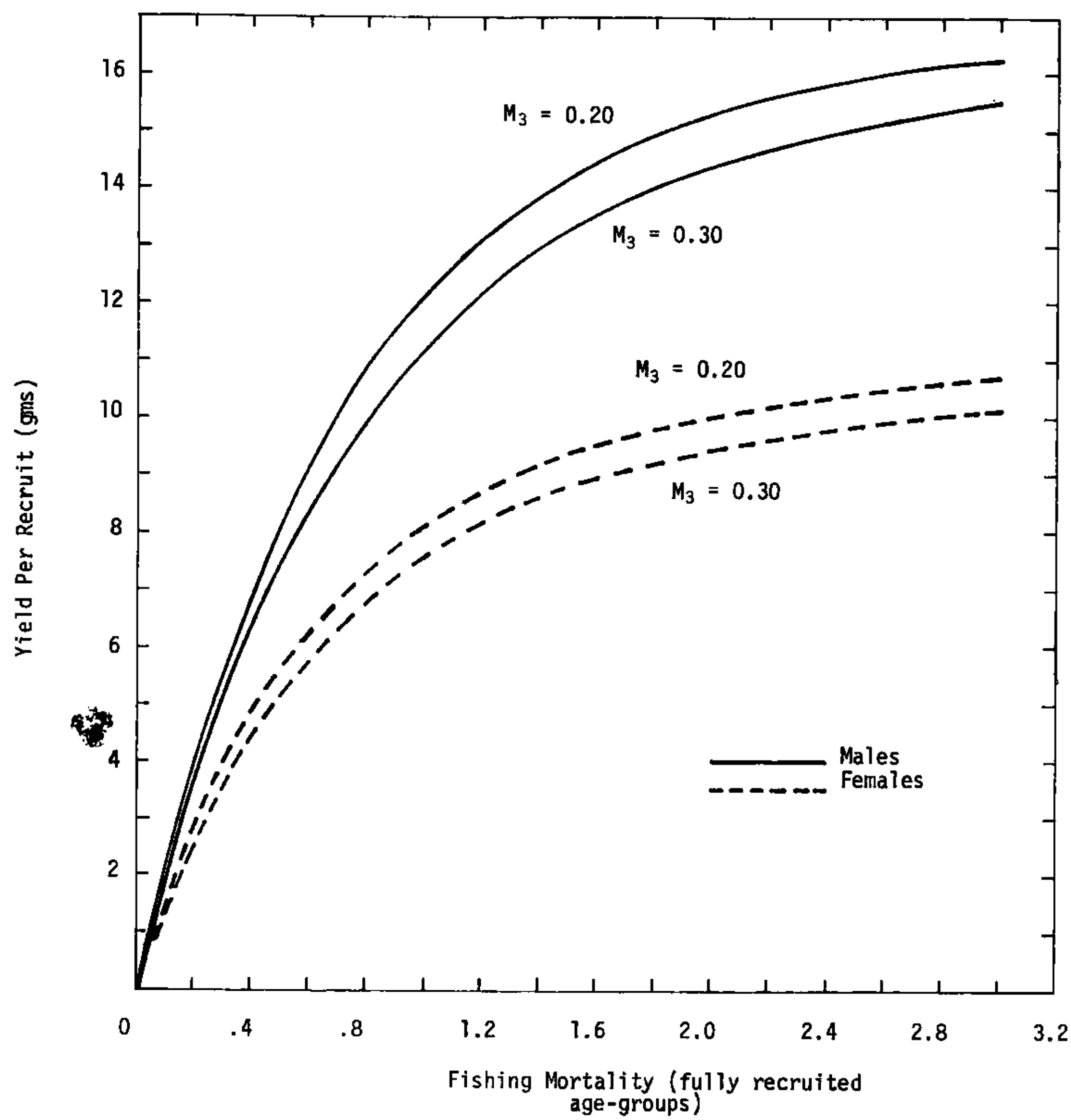

Fig. 15. Yield per recruit curve of Grand Bank capelin (M_3 = natural mortality rate at age 3).