An Indirect Method of Estimating Maturation Rates of Cohorts of Capelin (*Mallotus villosus*)

J. E. Carscadden, G. H. Winters and D. S. Miller
Fisheries Research Branch, Department of Fisheries and Oceans
Northwest Atlantic Fisheries Centre, P. O. Box 5667
St. John's, Newfoundland, Canada A1C 5X1

Abstract

A method of calculating age-specific maturation rates for capelin (*Mallotus villosus*) off southern Labrador and northeastern Newfoundland from catch-per-unit-effort data is presented. The data indicate that most of the capelin have matured at age 4. Underestimates of the instantaneous rates of either natural mortality or spawning mortality result in overestimation of the proportions of mature capelin by age-group, and overestimates of these mortality rates result in underestimation of the proportions of mature fish. In all cases, the percent error in proportions of mature capelin by age-group is considerably less than the percent error in the natural mortality or spawning mortality rate.

Introduction

The capelin stocks of the Northwest Atlantic were subjected to exploitation on an unprecedented scale during the 1970's, with catches in excess of 200,000 (metric) tons during 1973–77 and peak catches exceeding 360,000 tons in 1975 and 1976 (NAFO, 1984). Initially, the capelin fisheries in NAFO Subareas 2 and 3 were regulated by catch quotas which were based on crude predator-prey models (Winters and Carscadden, 1978). Subsequently, the quotas were derived from biomass estimation procedures which were based on either acoustic surveys or sequential computation models (Carscadden and Miller, MS 1979; Miller and Carscadden, MS 1979). The sequential computation models require estimates of a variety of population parameters, including age-specific and time-specific maturation rates. In addition, estimates of annual maturation rates are necessary for prediction of biomass levels of mature capelin which are available to the coastal fisheries. Direct estimates of annual maturation rates of capelin are difficult to obtain due to the segregation of mature and immature fish and also to the nature of the commercial fisheries which are based mainly on mature fish. In this paper, a method of calculating annual age-specific maturation rates from catch-per-unit-effort data for the capelin fisheries off southern Labrador and northeastern Newfoundland is presented.

Methodology

Although there is little direct information on the seasonal migration patterns of capelin in NAFO Divisions 2J and 3K (Fig. 1), some researchers (Kovalyov and Kudrin, 1973; Seliverstov and Serebrov, MS 1979) have suggested a general overwintering migration

from Div. 2J to Div. 3K during the autumn. This conclusion was based mainly on the temporal and spatial distributions of catches by fishing vessels, complemented by research vessel data. Because there are no offshore spawning areas in Div. 3K, it may be inferred
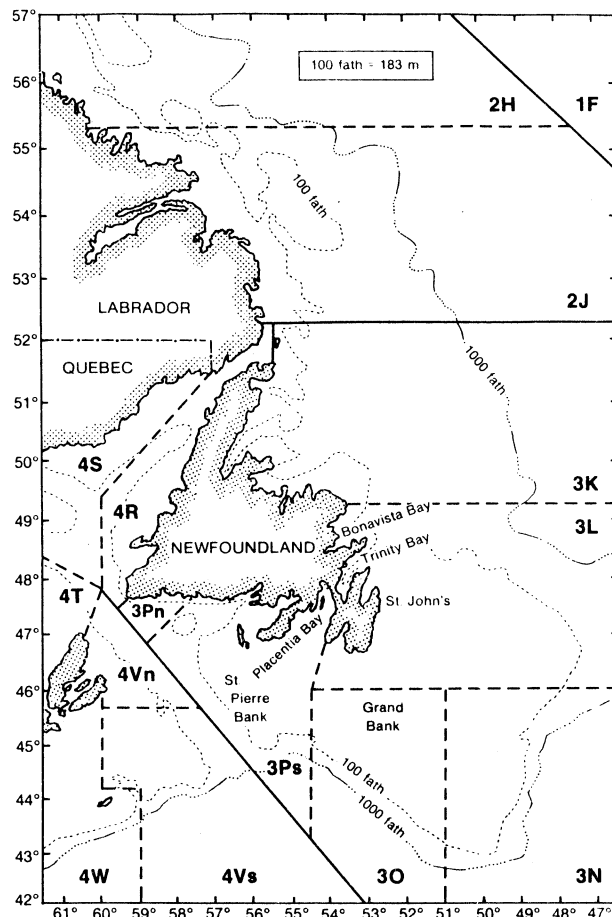

Fig. 1. Map showing NAFO Divisions referred to in the text.

that some of the migrating fish are mature and will spawn on the beaches of northeastern Newfoundland (Div. 3K) in the subsequent year. Sampling data, on file at the Northwest Atlantic Fisheries Centre, St. John's, Nfld., indicate that more than 99% of the offshore catches (age 2 and older) in Div. 2J and 3K during 1978 and 1979 were maturing fish. Furthermore, the similarity of the age compositions of offshore catches in Div. 2J and 3K in the autumn to those of spawning capelin on the inshore beaches of Div. 3K in the following summer during the 1973–77 period (Table 1) indicates that a large proportion of the offshore catches are maturing or mature fish.

From the above, the rate of recruitment (i.e. partial recruitment rate) can be considered to be equivalent to the age-specific maturation rate. If a time series of catch-per-unit-effort (CPUE) data is available, it is therefore possible to calculate the total instantaneous mortality rate (Z_t) of a year-class from time t to time t+1 by the equation

$$Z_t = \ln \left\{ (CPUE_t \times p_{t+1})/(CPUE_{t+1} \times p_t) \right\} \quad (1)$$

where $CPUE_t$ and $CPUE_{t+1}$ are catch rates of a year-class in years t and t+1 respectively, p_t is the mature proportion of a year-class during the autumn fishery in year t (equivalent to partial recruitment rate) and therefore the proportion of the year-class that will spawn in the following summer, p_{t+1} is the proportion of the same year-class that will be mature during the autumn fishery in year t+1, and ln refers to natural logarithms.

The total instantaneous mortality rate of a cohort from time t to time t+1 may also be defined as

$$Z_t = -\ln (N_{t+1}/N_t)$$

where N is comprised of both mature fish (pN) and immature fish ((1−p)N). Therefore, if S_t is the instantaneous spawning mortality rate in year t and M_t is the instantaneous natural mortality rate attributable to deaths other than spawning,

$$N_{t+1} = N_t \left\{ p_t\, e^{-(M+S_t)} + (1 - p_t)e^{-M} \right\}$$
$$= N_t\, e^{-M} \left\{ p_t\, e^{-S_t} + (1 - p_t) \right\}$$
$$\text{and } Z_t = M - \ln \left\{ p_t e^{-S_t} + (1 - p_t) \right\} \quad (2)$$

Therefore, if S_t, M and p_{t+1} are known or assumed for a particular age-group, there is a unique solution of equations (1) and (2) for Z and p_t. The estimation of

these parameters is started on the oldest age-class of a cohort and the unique value of p_t then becomes p_{t+1} in the sequential computation of the cohort's maturation history.

To illustrate the calculation of maturation rates, assumptions were made concerning the values of M and p_{t+1}. The natural mortality rate of capelin in the Northwest Atlantic is unknown, although an unsuccessful attempt was made to calculate M by an Icelandic technique (Carscadden and Miller, MS 1980). Thus, for use in this paper, M was assumed to be 0.3 for all age-groups.

Because the sequential calculation of maturation rate begins at the oldest age, p_{t+1} for age 7 fish was assumed to be 1.0. This assumption appears to be valid in view of the absence of older fish in the catch-at-age data (see Table 3) and the mean length of older fish relative to the length-maturity ogives (Carscadden, 1978).

Estimated or assumed values of spawning mortality (S_t) must also be available to calculate annual estimates of maturity. For use in this paper, age-specific S_t values were estimated from equation (2) by using Z values from Winters and Campbell (MS 1974). This type of calculation may appear to be somewhat circular because estimates of p and M are necessary to calculate S_t from equation (2). However, this approach was considered to be justified for two reasons: (a) there are no estimates of spawning mortality and the empirically-derived estimates provide relative age-specific values, and (b) the values of S_t are used only to illustrate the method of calculating maturation rates.

The effects of bias in the computed estimates of the proportions of mature capelin due to possible errors in the values of instantaneous natural mortality (M) and spawning mortality (S_t) were examined for arbitrary changes of ±33.3% in both M and S_t.

Capelin samples from Canadian research vessel catches on the Grand Bank (Div. 3LNO) (Northwest Atlantic Fisheries Centre, St. John's, Nfld., unpubl. data) were used to estimate total mortality rates (Z_t) for sexes combined after weighting by sex ratios (Table 2). Additional estimates of Z_t were calculated from equation (1) with the use of USSR catch-at-age data (sexes

TABLE 1. Percentage age compositions of capelin from the autumn fishery (A) in Div. 2J and 3K and the subsequent summer spawning population (S) in Div. 3K during 1972–77, with the autumn frequencies incremented by 1 year.

Age (yr)	1972–73 A	1972–73 S	1973–74 A	1973–74 S	1974–75 A	1974–75 S	1975–76 A	1975–76 S	1976–77 A	1976–77 S
3	12	2	25	31	20	40	62	61	9	2
4	64	90	30	46	49	53	28	38	83	92
5	21	8	40	20	18	5	8	1	7	5
6+	3	1	5	3	13	2	2	1	1	1

TABLE 2. Estimated total mortality rates (Z_t) for capelin from unpublished Canadian and USSR sampling data, and age-specific spawning mortalities (S_t) estimated from p-values of Winters and Campbell (MS 1974).

	Estimated Z_t values				S_t values
Age (yr)	Canadian data	USSR data	Mean	Age (yr)	Mean
3–4	0.73	0.60	0.67	3	1.39
4–5	2.11	1.17	1.64	4	1.69
5–6	2.23	2.83	2.53	5	2.23

combined) for Div. 3L(V. S. Bakanev, PINRO, Murmansk, pers. comm.) and the age-specific maturation rates of Winters and Campbell (MS 1974). The mean Z_t values from the Canadian and USSR data (Table 2), the maturation rates (p_t) of Winters and Campbell (MS 1974), and the assumed natural mortality rate (M = 0.30) were then used in equation (2) to derive age-specific spawning mortalities (S_t). The value of 2.23 was assumed to be the spawning mortality of age 5 and older capelin.

The catches of capelin (numbers) by age-group for 1972–78 (Table 3) were derived from USSR sampling data (A. S. Seliverstov, PINRO, Murmansk, pers. comm.) and the catch rates were from Seliverstov and Serebrov (MS 1979). The 1979 catches by age-group were derived from data which were collected by Canadian observers aboard USSR fishing vessels.

Results and Discussion

For nearly all year-classes of capelin in Div. 2J and 3K (Table 4), the peak in CPUE occurred at age 3 (spawning age 4), which is the age at which most individuals of a year-class mature for spawning. Furthermore, the CPUE values were highest for ages 2–4 of the 1973 year-class, indicating that it was the strongest of the year-classes that were sampled during 1972–79.

Instantaneous total mortality rates (Z_t), unadjusted for annual changes in partial recruitment, indicate that some year-classes may not be completely mature until age 7 (Table 4). The anomalous values of Z_t for the older age-groups of the 1971 and 1972 year-classes were probably due to errors in ageing the older fish and/or to inadequate sampling of age-groups 5 and 6 in 1977.

The age-specific maturation rates (Table 5), which correspond to the unique solutions of equations (1) and (2), were calculated from the CPUE data in Table 4, with the assumptions that natural mortality was 0.3 and that all 7-year-old capelin were fully mature. The maturation rates for each age-group varied considerably among year-classes. Such variation may not be surprising when one considers the probable influence of variable growth rates on maturation rates, and these growth rates may in turn be affected by a complex of factors which include large fluctuations in year-class size and variable hydrographic conditions. Nevertheless, the mean values increased progressively with age.

Although the present analysis was intended to be an illustration of how maturation rates can be derived from catch-per-unit-effort data, some guidance in evaluating the method was provided by means of estimates of the proportions of mature capelin from other sources. Such estimates (Table 6) were derived by

TABLE 3. Age composition of capelin catches (millions of fish) and catch-per-unit-effort (tons/hr) for the autumn fishery by USSR trawlers in Div. 2J and 3K, 1972–79.

Age (yr)	1972	1973	1974	1975	1976	1977	1978	1979
2	228.4	1,306.4	1,015.2	5,540.0	789.7	157.0	247.5	355.5
3	1,240.1	1,538.8	2,463.9	2,486.9	7,409.4	1,578.1	842.8	47.3
4	406.4	2,085.3	888.1	733.3	605.7	3,170.4	574.8	11.0
5	54.7	262.2	616.2	164.8	77.4	328.8	581.1	15.4
6	7.2	14.2	49.3	43.0	16.3	45.1	28.3	14.2
CPUE	2.81	3.29	4.56	6.47	5.27	4.14	2.29	1.34

TABLE 4. Catch-per-unit-effort (CPUE) and resultant total mortality rates (Z_t) for the 1966–77 year-classes of capelin in the USSR autumn fishery in Div. 2J and 3K during 1972–79. (Mortality rates are unadjusted for annual changes in partial recruitment; add 1 year to obtain the spawning age for CPUE data.)

Year-class	CPUE by age-group (No. $\times 10^{-3}$/hr)					$Z_t = \ln (CPUE_t/CPUE_{t+1})$			
	2	3	4	5	6	2/3	3/4	4/5	5/6
1966					0.45				
1967				3.40	0.34				2.30
1968			25.25	6.32	1.77			1.39	1.27
1969		77.05	50.29	22.13	1.40		0.43	0.82	2.76
1970	14.19	37.11	31.90	5.37	0.40	-0.96	0.15	1.78	2.60
1971	31.51	88.51	23.91	1.88	1.23	-1.03	1.31	2.54	0.42
1972	36.47	81.06	14.75	8.97	1.23	-0.80	1.70	0.50	1.99
1973	181.03	180.51	88.53	22.59	1.97	0.00	0.74	1.34	2.44
1974	19.23	43.07	25.07	2.14		-0.81	0.54	2.46	
1975	4.29	36.75	1.53			-2.15	3.18		
1976	10.79	6.56				0.50			
1977	49.28								

TABLE 5.   Estimated maturation rates (p_t) of the 1967–73 cohorts of capelin in Div. 2J and 3K, based on data from the USSR fishery in 1972–79.

Year-class	Maturation rates by age-group			
	3	4	5	6
1967				0.97
1968			0.76	0.79
1969		0.48	0.67	1.00
1970	0.12	0.47	0.89	1.00
1971	0.19	0.83	0.93	0.57
1972	0.22	0.80	0.56	0.93
1973	0.34	0.62	0.80	0.99
Mean	0.22	0.64	0.77	0.89

TABLE 6.   Percentages of mature capelin by age based on back-calculated lengths in inshore samples from Div. 3K and maturity ogives for samples from the Grand Bank.

Age (yr)	Male		Female		Sexes combined
	Length (mm)	Percent mature	Length (mm)	Percent mature	
3	145	~5	128	~5	~5
4	170	55	153	75	65
5	189	100	172	100	100
6	202	100	187	100	100

using back-calculated lengths of capelin from Notre Dame Bay (Div. 3K) (Winter, 1982) and maturity ogives for capelin from the Grand Bank (Div. 3LNO) (Carscadden, 1978). The trends in maturation rates are similar, with relatively few capelin being mature at age 3 and all of the fish being mature at age 5. In view of the assumptions relevant to calculation of the maturation rates in this paper and because both methods are subject to sampling error, the estimates in Table 6 are considered to support the method of estimating maturation rates from CPUE data.

Changes in assumed values of natural mortality (M) by ±33.3% resulted in similar trends of p_t for all year-classes (Fig. 2), there being a progressively larger effect on p_t with decreasing age. The largest changes were for age-group 3, with p_t being overestimated by 10–17% for the decreased value of M and underestimated by 8–14% for the increased value of M. The trend of increasing difference with decreasing age is probably connected with the sequential nature of the computations, with the calculations proceeding from the oldest to the youngest age-group.

Similar trends of increasing error in p_t with decreasing age were exhibited by ±33.3% changes in spawning mortlity (S_t) (Fig. 3). The errors in p_t were greater when S_t was decreased than when S_t was increased, the ranges being 16–18% and 8–10% respectively.

The analysis in this paper ignores the effect of fishing mortality in the calculation of p_t values from the catch-curve generated Z_t values. If the assumed value of M is correct, the non-adjustment of Z_t values to account for the effect of fishing mortality (F) would lead to a positive bias in the estimates of p_t. Although M was assumed to be constant in analyzing the 1972–79 capelin data, the major cod stock of the area (Div. 2J+3KL), which preys heavily on capelin (Winters and Carscadden, 1978), declined greatly during the same period (Wells, MS 1981). Thus, M for capelin may have declined during the 1970's. However, exploitation of capelin increased substantially during this period, and

this may have compensated for the decreased mortality due to cod predation. Therefore, the potential bias in the analysis, due to non-adjustment of Z for fishing mortality (F), may not be significant, because F could be considered as being included in the assumed M value. Unfortunately, the effects of F cannot be taken into account in greater detail because there are no independent estimates of fishing mortality.

Leggett et al. (1984) have contended that fishing mortality was not important in explaining trends in abundance of capelin during the 1970's. Part of their evidence was a comparison of catches and trends in abundance which were derived from sequential abundance models with the use of estimates of p_t as derived in this paper. Therefore, their evaluation of fishing mortality is not relevant in the present context. However, the main results of their paper showed a correlation between year-class survival of capelin and environmental variables. They found that 58% of the variation in year-class strength could be explained by the frequency of onshore winds during the beach residence of larvae and temperature of the near-surface (0–20 m) water layer during 6 months after larval emergence. These results were obtained from data which were collected during the period of heaviest exploitation of capelin in the 1970's and indicate that more attention should be focused on estimating natural mortality rather than fishing mortality for use with the presented method of calculating proportions of mature capelin by age group.

The accuracy of maturation rates (p_t) depends greatly on the catch-per-unit-effort and sampling data for which there are no estimates of variance. Ulltang (1980) noted that catch-per-unit-effort estimates from a pelagic fishery with gears other than purse-seine may provide better abundance indices, although data from aimed trawling may exhibit biases similar to those from a purse-seine fishery. One of the most common biases in purse-seine data involves the catchability of shoaling species, whereby catchability increases with declining stock size, and, as a result, catch-per-unit-effort does not decline and therefore does not reflect the status of the stock. The CPUE data for the capelin stock in Div. 2J+3K show considerable variation (five-fold change between the highest and lowest values),
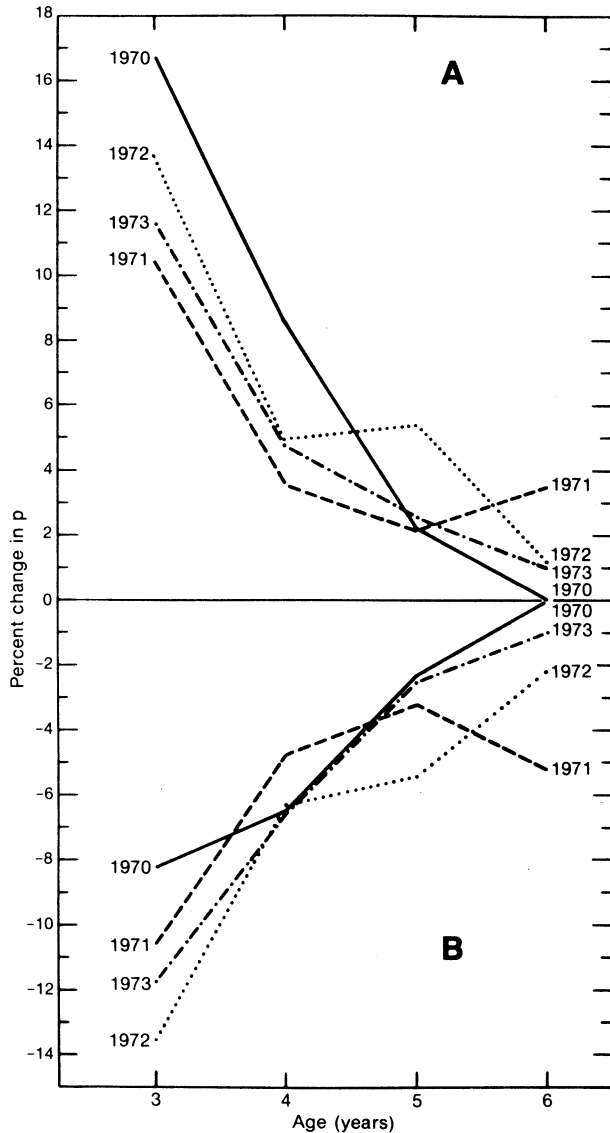
Fig. 2. Percent changes in proportion (p$_t$) of mature capelin of the 1970-73 year-classes by age-group when natural mortality (M) is reduced by one-third (**A**) and increased by one-third (**B**).
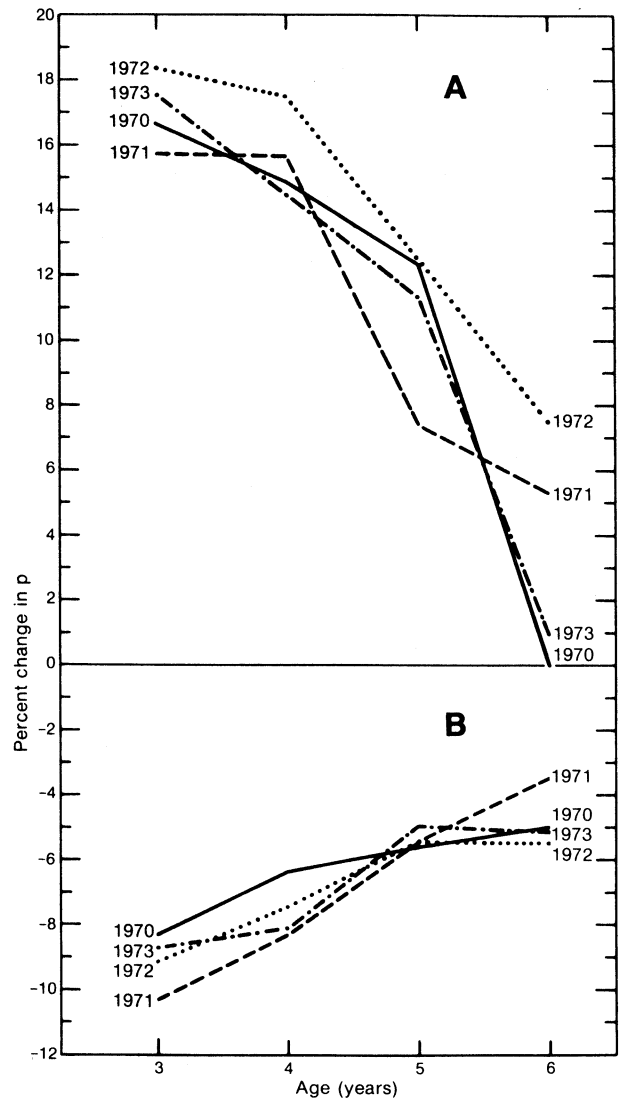

Fig. 3. Percent changes in proportions (p$_t$) of mature capelin of the 1970-73 year-classes by age-group when spawning mortality (S$_t$) is reduced by one-third (**A**) and increased by one-third (**B**).

indicating that these estimates may be a reasonable reflection of changes in the stock. In fact, these data have been used as abundance indices in assessing the capelin stocks (NAFO, 1983).

The sensitivity of the sequential computation model to changes in maturation rates (p$_t$) are unknown. In an earlier version of the model (Miller and Carscadden, MS 1979), a change in p$_t$ of 1% resulted in a change of 2.8% in the total population. Thus, such models are potentially sensitive to changes in maturation rate, and this aspect will have to be addressed when evaluating the sequential computation model for capelin.

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