

Age- and Sex-Specific Survival of Northern Grand Bank Capelin (*Mallotus villosus*)

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Age-specific, sex-specific survival rates for immature and mature capelin (*Mallotus villosus*) were estimated by linear least-squares models, using abundance data derived from annual acoustic/trawl research surveys conducted from 1982 to 1990 on the northern Grand Bank. Survival estimates for age 2 immature fish were comparable between sexes (annual survival equals approximately 40%). Survival estimates for age 4 mature fish differed between sexes, with females having a higher (25–51%) average survival estimate than males (6%). Survival estimates for immature and mature age 3 fish were equivocal; immature males and females had comparable rates (30.3–32.3 and 15.2–26.6%, respectively) whereas a greater proportion of mature females (25–50%) survived than of mature males (2.5–13%). The stated ranges denote survival estimates including and excluding an influential data point, respectively. Higher average survival of mature females than of mature males may be a result of sex-specific behavior during beach spawning. The average annual contribution of surviving mature females to the total number of female spawners was estimated as 24–47%.

Nous avons calculé les taux de survie spécifiques à l'âge et au sexe pour les capelans (*Mallotus villosus*) immatures et matures par des modèles linéaires des moindres carrés, en nous servant des données sur l'abondance tirées de relevés annuels de recherche menés par des méthodes acoustiques et au chalut, de 1982 à 1990, sur le nord du Grand Banc. Les taux de survie estimés pour les poissons immatures d'âge 2 étaient comparables d'un sexe à l'autre (le taux annuel de survie est égal à environ 40 %). Les taux de survie estimés pour les poissons matures d'âge 4 différaient entre les sexes, celui des femelles étant supérieur en moyenne (25–51 %) à celui des mâles (6 %). Les taux de survie estimés pour les poissons immatures et matures d'âge 3 étaient équivoques; les mâles immatures et matures avaient des taux comparables (30,3–32,3 et 15,2–26,6 % respectivement), tandis qu'une proportion plus forte de femelles matures (25–50 %) survivaient par rapport aux mâles matures (2,5–13 %). Les fourchettes ainsi établies indiquent que les estimations du taux de survie incluent ou excluent un point de données d'importance. Le fait que le taux moyen de survie des femelles matures soit plus élevé que celui des mâles matures peut être lié à un comportement spécifique au sexe pendant la ponte sur les grèves. On estime à 24–47 % la proportion annuelle moyenne des femelles matures survivantes par rapport au nombre total de génitrices.

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Capelin (*Mallotus villosus*) is an abundant cold-water fish inhabiting northern oceans around the globe. It is generally characterized by small body size, short generation time, high variability in population size, and semelparity. On the basis that capelin is a principal forage species in northern ecosystems, it is possible that semelparity evolved in response to a high adult mortality rate. However, postspawning survival may occur in the Northwest Atlantic Ocean. Females have been observed with residual eggs 4–5 mo after the spawning period (Templeman 1948; Winters 1971), and the inshore fishery data consistently show higher proportions of females than males at the oldest ages (Nakashima and Harnum 1992). The possibility of iteroparous female capelin is intriguing from both a life history perspective, in that a sex-specific life history strategy may have evolved, and a fishery perspective, in that iteroparous individuals contribute to the spawning stock and fishery. We adopt a fishery perspective in this paper.

It has been difficult to estimate the degree of iteroparity in Northwest Atlantic populations of capelin in the absence

of separate survival estimates of immature and mature fish. Carscadden et al. (1985) indirectly estimated spawning mortality by using the average total mortality rate estimated from Canadian and Russian catch data, the proportions mature estimated in Winters and Campbell (1974), and assuming a natural mortality of 0.3 for all age groups. However, the authors emphasized that the spawning mortality estimates may be imprecise and were derived to demonstrate the primary topic of the paper, which was an indirect method of estimating capelin maturation rates.

Recently, Shelton et al. (1993) used the acoustic/trawl research survey data of Miller and Carscadden (1991), in which the proportions of mature fish were estimated directly, to estimate average annual survival rates separately for immature and mature capelin from the northern Grand Bank. In this paper, we show that much of the residual variability from the fit of the model in Shelton et al. (1993) is accounted for by age and sex, and we use those results to estimate the contribution of iteroparous individuals to the total spawning stock.

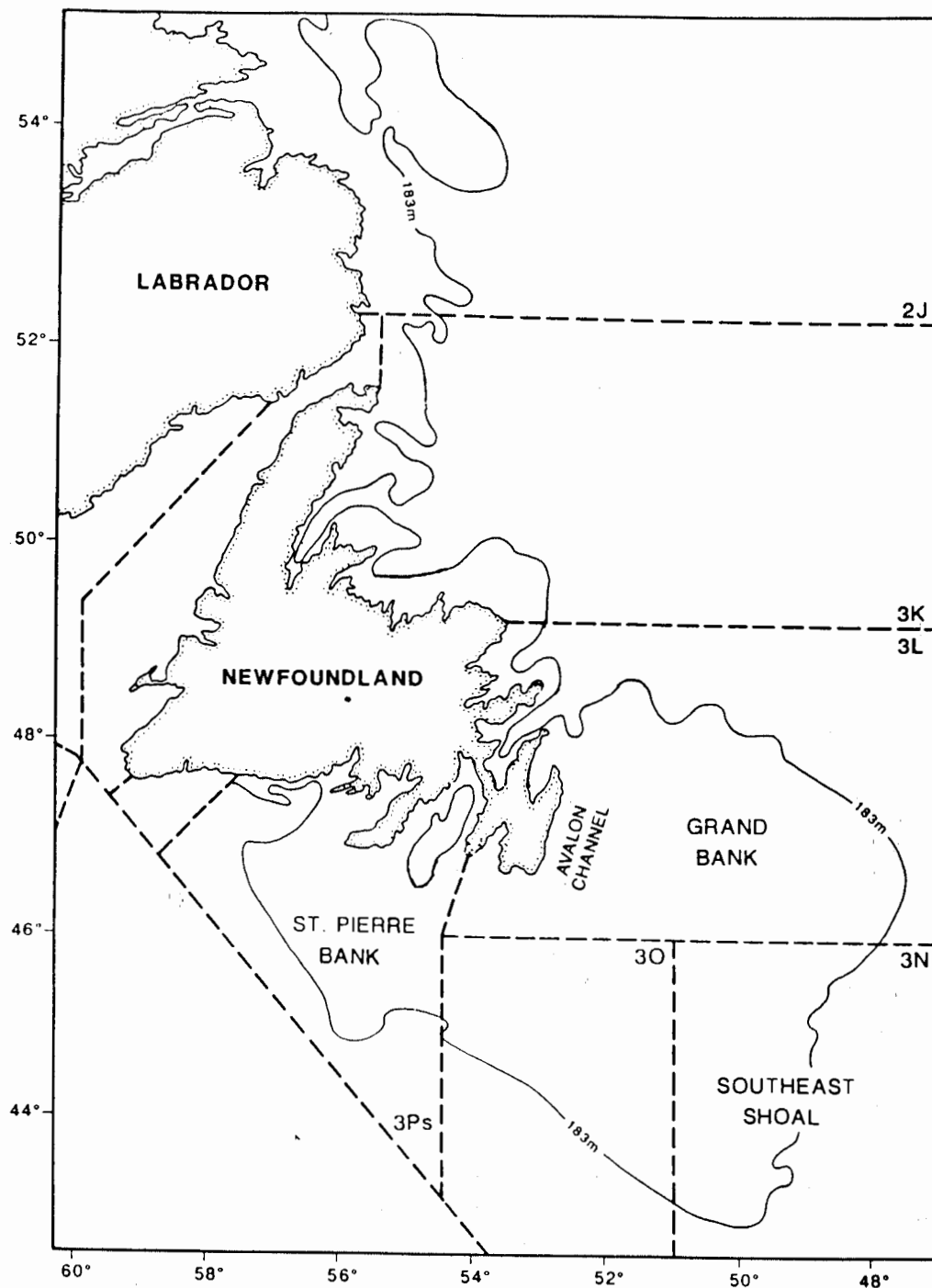


FIG. 1. NAFO Divisions: annual acoustic/trawl surveys. Approximate boundaries of survey area: 46°N to 49°N, 49°30'W to 52°45'W.

Material and Methods

Acoustic/Trawl Research Survey Database

Annual acoustic surveys of capelin are conducted for the purpose of recommending total allowable catches based on a projection of the numbers of mature capelin expected inshore in the following year (see Miller and Carscadden 1991). The survey area was located on the northern Grand Bank, roughly bounded by 46°N to 49°N and 49°30'W to 52°45'W, within Northwest Atlantic Fisheries Organization Division 3L (NAFO Div. 3L) (Fig. 1). Acoustic survey methods (data acquisition/echo integration systems, calibration

parameters, etc.) and survey design are described in Miller (1985) and Miller and Carscadden (1989, 1991).

Midwater trawls were used to verify species identity and sample capelin length, age, and maturity throughout the survey area each year. Two hundred fish per trawl were randomly sampled and their lengths measured. From this random sample, stratified samples of two fish per half-centimetre group for each sex were used to construct age-length relationships. Length composition and the age-length key were used to determine the age composition in subdivided areas (strata) within the larger survey area. Total survey age composition and proportion of mature fish for each year were calculated by weighting each stratum by its estimated biomass.

TABLE 1. Numbers-at-age (millions) (*N*) and percent mature (*P*) of males and females for 1982–90 at ages 2–6 as estimated from the acoustic/trawl surveys. The total of each *N* column denotes the sum over all years; the total of each *P* column denotes % (total number of mature animals/total *N*). The average is the sum of *P*/total number of years.

Year	Age (yr)									
	2		3		4		5		6	
	<i>N</i>	<i>P</i>	<i>N</i>	<i>P</i>	<i>N</i>	<i>P</i>	<i>N</i>	<i>P</i>	<i>N</i>	<i>P</i>
<i>Males</i>										
1982	4.13	4.82	7.83	74.51	0.63	95.95	0.19	97.98	0.00	0.00
1983	1.68	1.15	0.81	30.14	0.25	94.61	0.00	—	0.00	0.00
1984	9.31	2.38	2.32	68.86	0.98	98.06	0.07	98.30	0.00	0.00
1985	168.37	0.48	35.63	27.63	0.91	82.54	0.15	100.00	0.00	0.00
1986	32.68	0.17	73.01	20.52	7.12	90.67	0.00	—	0.00	0.00
1987	40.75	0.29	6.89	40.96	18.09	99.06	0.48	99.41	0.00	0.00
1988	176.58	0.67	34.01	65.53	5.98	100.00	1.13	100.00	0.00	0.00
1989	138.89	0.17	39.73	34.12	3.92	97.63	0.00	—	0.00	0.00
1990	161.21	0.26	62.24	21.84	18.76	94.25	0.11	100.00	0.00	0.00
Total	733.59	0.44	262.47	32.29	56.64	96.08	2.14	99.63	0.00	0.00
Average <i>P</i>		1.15		42.68		94.75		99.28		0.00
<i>Females</i>										
1982	5.42	9.06	8.28	87.69	1.74	97.66	0.58	99.26	0.18	99.55
1983	1.74	23.43	1.12	73.38	0.52	90.29	0.06	86.62	0.00	—
1984	11.73	13.43	3.90	93.94	2.16	99.23	0.39	99.66	0.02	98.12
1985	201.15	4.84	44.84	56.04	2.89	92.33	2.14	100.00	0.03	100.00
1986	26.69	1.35	85.05	50.18	14.17	94.82	0.71	100.00	0.31	100.00
1987	47.32	2.71	11.41	96.82	20.83	99.75	3.43	99.76	0.08	100.00
1988	203.86	3.08	31.64	87.83	3.69	97.97	14.17	99.21	1.53	100.00
1989	175.83	2.45	56.43	62.01	7.13	97.79	0.43	97.25	0.96	100.00
1990	191.96	6.88	106.72	68.93	36.84	97.17	1.85	65.31	0.00	—
Total	865.71	4.35	349.39	64.95	89.95	97.34	23.76	96.69	3.10	100.00
Average <i>P</i>		7.16		74.18		96.44		94.38		99.96

We used information from surveys conducted in April–May, just prior to the inshore spawning migration, from 1982 to 1990. In April and May, the gonads of mature and immature capelin are visually distinguishable. Estimates of proportions of mature fish and numbers-at-age (Table 1) were used to calculate age-specific, sex-specific survival rates.

The population structure of capelin off the Newfoundland and Labrador coasts is unresolved. The regulatory agencies use the current designation of two to three separate spawning populations along a north–south gradient, but that designation is based largely on circumstantial evidence (summarized in Nakashima 1992). A recent study of capelin migration patterns indicated that mature capelin from northern (NAFO Div. 3K) and southern (NAFO Div. 3L) areas may be mixing during their spawning migration (Nakashima 1992). Nonetheless, capelin in NAFO Div. 3L are still treated as a separate unit stock for management purposes.

Gulland (1983) stated that “a group of fish can be treated as a unit stock if possible differences within the group and interchanges with other groups can be ignored without making the conclusions reached [from the model] depart from reality to an unacceptable extent.” For the purpose of estimating survival rates, we could assume that capelin in the 3L survey area behaved as a unit stock for the following reasons. The average annual age structure estimated from

the research trawls consists of few 1-yr-olds, abundant 2-yr-olds, followed by decreasing abundances of ages 3, 4, 5, and 6. Thus, the offshore samples are not representative of the abundance of fish less than 2 yr old (Nakashima 1990). In contrast, abundance estimates of males and females of ages 2–6 were judged consistent over time on the basis that strong (relatively abundant) year classes in year *t* corresponded to strong year classes in year *t* + 1. Further, acoustic abundance estimates of mature capelin are correlated with inshore fishery catch rate data a few months later (Carscadden 1992).

We could assume the survey data were representative of a single stock until 1991, in which year the capelin biomass detected in the acoustic survey was exceedingly low and the estimated age distribution changed dramatically relative to former years (Miller and Carscadden 1991). Capelin in 1991 were suspected to have been missed by the acoustic survey perhaps because of a change in capelin distribution. Thus, we assume that the annual acoustic surveys were representative of the stock of ages 2–6 in the northern Grand Bank stock for the years 1982–90 only.

Survival Estimation

Shelton et al. (1993) proposed a simple model for the survival of capelin cohorts on the basis that the fishery captures mature fish only:

TABLE 2. Age-specific, sex-specific survival rates of the northern Grand Bank capelin stock as estimated by linear regression. R^2 is the amount of variability explained by model (2) for ages 2, 4, and 5 and Model (1) for age 3. S is the regression coefficient (estimate of survival rate). SE is the standard error of the regression coefficient. $n = 8$ for each analysis except $n = 7$ in analyses excluding an influential datum.

	R^2	S	SE
Age 2			
Male	0.826	0.366	0.064
Female	0.853	0.428	0.067
Age 3			
Male	0.854		
Immature		0.322	0.100
Mature		0.130	0.216
Female	0.816		
Immature		0.152	0.360
Mature		0.497	0.273
Age 3, excluding influential datum			
Male	0.944		
Immature		0.303	0.050
Mature		0.025	0.111
Female	0.973		
Immature		0.266	0.089
Mature		0.250	0.072
Age 4			
Male	0.896	0.057	0.007
Female	0.843	0.511	0.083
Age 4, excluding influential datum			
Female	0.853	0.250	0.042
Age 5			
Male		0	
Female	0.519	0.089	0.033

$$(1) N_{a+1,t+1} = N_{a,t}(1 - p_{a,t})S_i + (N_{a,t}p_{a,t} - C_{a,t})S_m + \epsilon_{a+1,t+1}$$

where N is the number of fish estimated from the acoustic survey, C is the commercial catch by number (taken during a fishery lasting about 4 wk), p is the proportion mature by number, S_i is the average annual (finite) survival rate of immature fish, S_m is the average annual (finite) survival rate of mature fish, and ϵ is randomly distributed error. The subscripts a and t denote age and year, respectively. Shelton et al. (1993) estimated S_i as 0.35 (SE = 0.043) and S_m as 0.227 (SE = 0.239). These results were considered practical for potential use in assessment models (Shelton et al. 1993).

It subsequently became apparent that the proportion of females increases with age. Below are the total numbers-at-age (millions) estimated from the acoustic/rawl surveys and summed over the years 1982–90 and percent female at each age from 2 to 6:

	2	3	4	5	6
Total abundance	1599.3	611.9	146.6	25.9	3.1
% female	54.1	57.1	61.4	91.7	100.0

Since the older age classes are largely mature and the sex ratio becomes progressively more skewed with age, it appears that mature females have a higher survival than mature males. Model (1) can be fitted separately to each sex or to each sex–age combination. Based on the predominance of females in older age classes, we (i) analyzed ages and sexes

separately and (ii) examined age–sex–year-specific survival rates.

Regression estimates

We first fitted equation (1) separately for each sex with all age groups combined. We then analyzed each sex–age combination. Since landings averaged only 4% of the predicted biomass from 1982 to 1990 (Shelton et al. 1993), we eliminated the catch term for simplicity. Most (>94%) 2-yr-old capelin are immature, so all fish were assumed immature in the analysis of survival of age 2 fish. Most (>96%) 4 and most (>97%) 5-yr-old capelin are mature; so all fish were assumed mature in the analysis of survival of 4- and 5-yr-olds. Survival rates of 2-, 4-, and 5-yr-olds were estimated separately for each age by sex from the simple regression model

$$(2) N_{a+1,t+1} = N_{a,t} S_i + \epsilon_{a+1,t+1}$$

where the symbols are as described previously.

Estimating survival of 3-yr-olds involved accounting for the varying proportion mature among years. Separate estimates for immature and mature 3-yr-olds for each sex were obtained from model (1) excluding commercial landings.

Survival ratios

Age-specific, sex-specific survival rates were estimated for each pair of adjacent years by computing the ratio of female, or male, capelin at a given age in a given year to the number of capelin at the previous age in the previous year ($N_{a+1,t+1}/N_{a,t}$).

Contribution of surviving mature females to the spawning stock

The relative contribution (RC) of surviving mature females to the total spawning stock from 1982 to 1990 was estimated from

$$(3) RC = \frac{\sum_{t=82}^{90} \sum_{a=3}^6 N_{a,t}^M S_{m,a}}{\sum_{t=82}^{90} \sum_{a=3}^6 N_{a,t}^M}$$

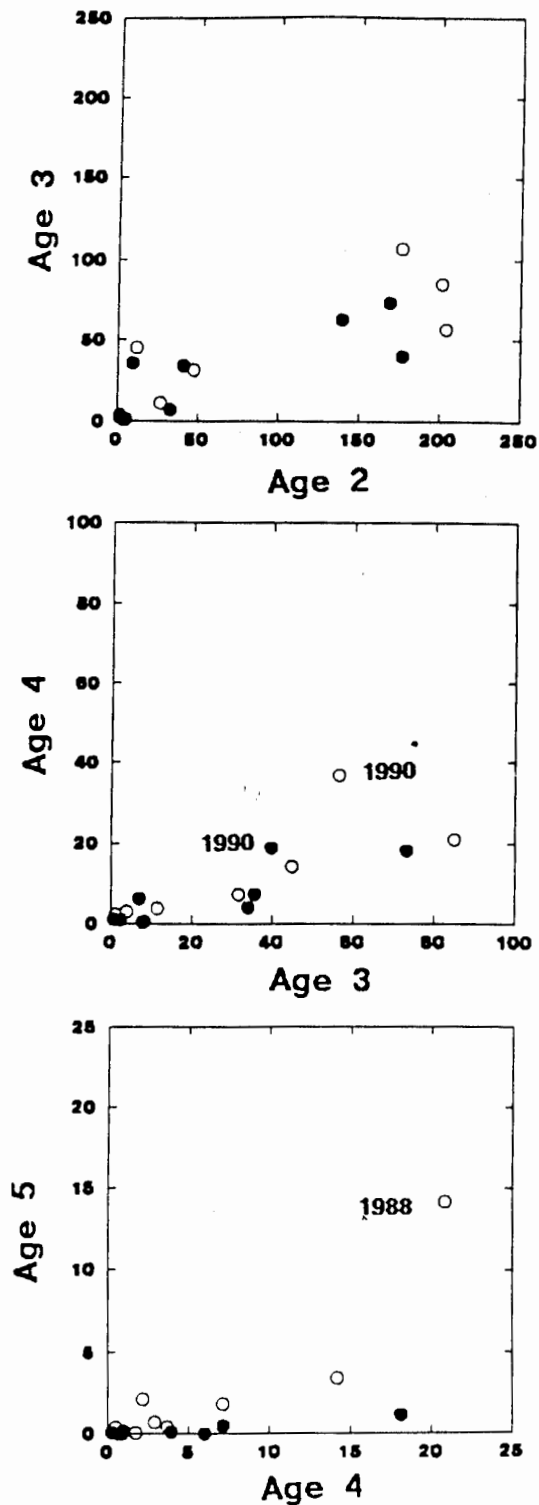
where $N_{a,t}^M$ is the number of mature females at age a in year t and $S_{m,a}$ is the survival estimate of mature females at age a . This is simply an estimate of the proportion of spawning females that will survive to the next spawning season averaged over the 9-yr period.

Results

When ages are combined, the sex-specific survival estimates ($n = 24$) are 0.427 (SE = 0.043) and 0.358 (SE = 0.194) for immature and mature females, respectively, and 0.365 (SE = 0.037) and 0.073 (SE = 0.280) for immature and mature males, respectively.

When ages are analyzed separately, survival of immature 2-yr-old male capelin does not appear to differ from that of immature 2-yr-old females (Table 2; Fig. 2–4). In the mature age classes, survival of age 4 females is higher than that of age 4 males. Annual estimates of survival (ratio of $N_{a+1,t+1}/N_{a,t}$) of age 4 females are consistently higher than those of males (Fig. 4, $p = 0.008$ for a two-sided sign test with $n = 8$ comparisons). The pattern for 3-yr-olds is less clear but consistent with the above. Overall, survival of

Number ($\times 10^6$) at Age + 1



Number ($\times 10^6$) at Age

FIG. 2. Number-at-age + 1 as a function of number-at-age for ages 2-5 for each sex. The 1988 and 1990 survey points are denoted as influential data points assuming a linear function between the dependent and independent variables (see text). Solid circles refer to males and open circles to females.

mature age 3 and 4 females appears to be higher than that of mature age 3 and 4 males. Further, there are virtually no males that survive from age 5 to 6 whereas a small fraction of females do (Table 1; Fig. 3).

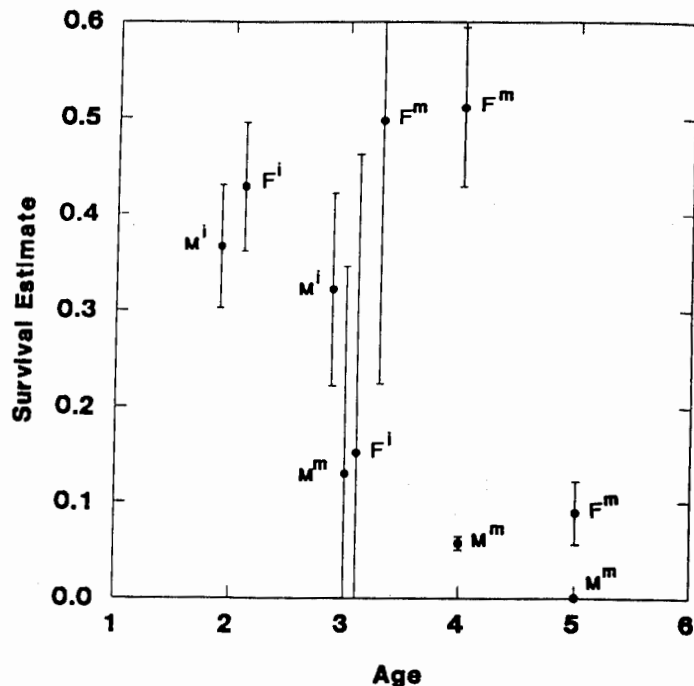


FIG. 3. Survival from age a to age $a + 1$, as estimated from models (1) and (2) described in the text. M^i refers to immature males, M^m to mature males, F^i to immature females, and F^m to mature females. Vertical bars are ± 1 SE.

Examination of the residual variation and original plots of dependent and independent variables made it apparent that one datum in each analysis of age 3 male and females and one datum in analysis of age 4 females were influencing survival estimates more than other data. Subsequent analyses excluding those data confirmed their influence. Given that the stability of our results is low partially due to the low number of data points, and that one datum can substantially change the results, we present survival estimates with and without the most influential datum. When age 3 females and males are analyzed without the most influential datum (labelled in Fig. 2), survival estimates change notably, standard errors become smaller, and the amount of variance explained increases (Table 2). The survival estimate for age 4 females drops from 0.511 (SE = 0.083; $n = 8$) to 0.250 (SE = 0.042; $n = 7$) when an influential datum (labelled in Fig. 2) is excluded from the analysis. Nonetheless, age 4 females still have a higher survival rate than males.

The relative contribution of surviving mature females to the total female spawning stock, as estimated from equation (3), is 47% when survival rates estimated from all the data were used and 24% when survival rates were estimated from data excluding the influential data points.

Discussion

Sex-Specific Survival

Survival of mature age 4 and 5 female capelin is clearly higher than that of mature males; whether differential survival between sexes occurs at age 3 is equivocal. Mature female capelin may survive longer than mature males as a result of differential spawning behavior. Male capelin typically rest close inshore waiting for females, who stay farther offshore until ready to spawn. Waiting males meet successive

Ratio of N_{t+1}/N_t

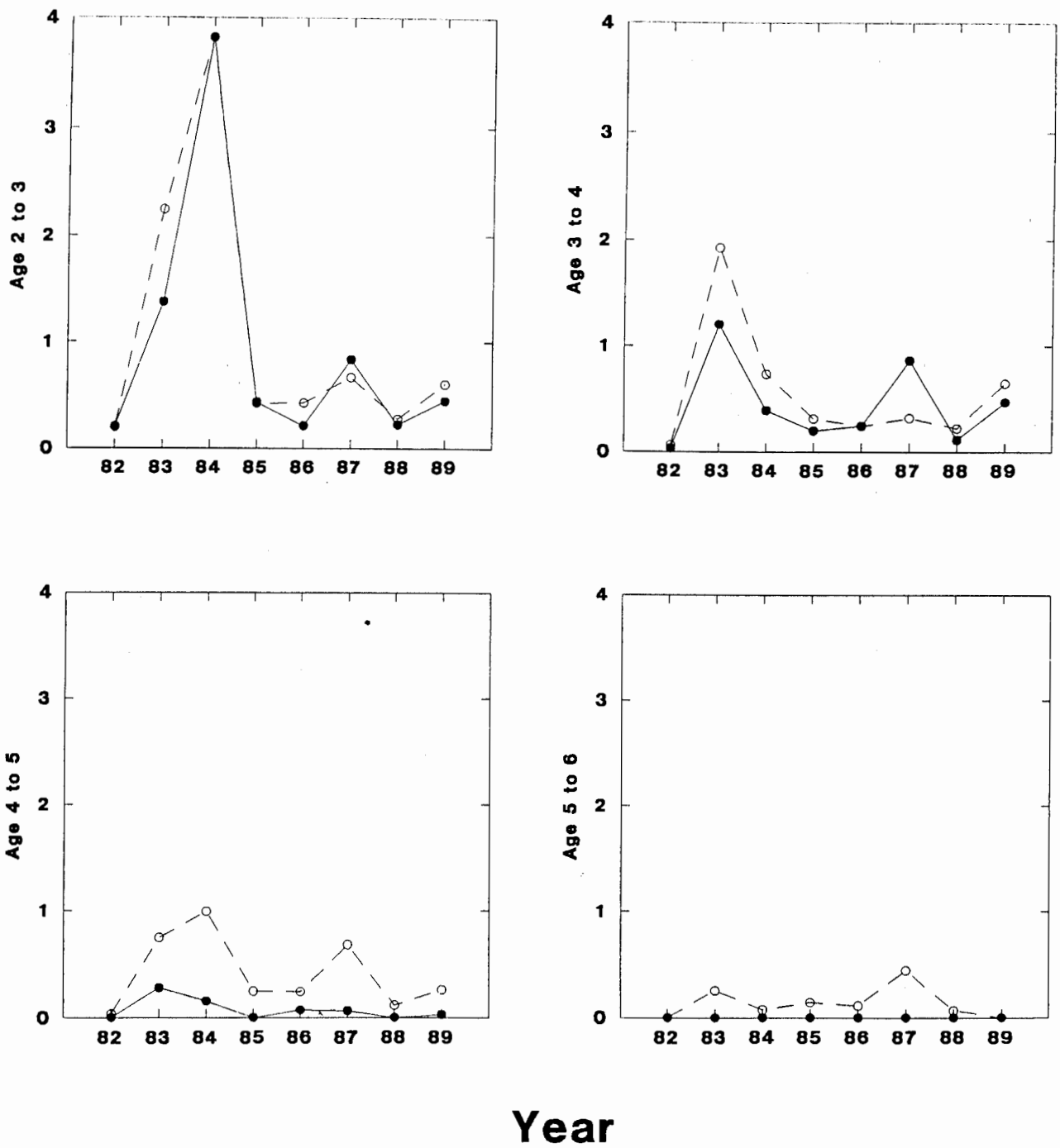


FIG. 4. Annual survival estimated as the ratio of $N_{a+1,t+1}/N_{a,t}$ of ages 2–5 plotted by year. Solid circles refer to males and open circles to females. Note that the survival estimate for females is consistently above that for males at ages 4–5 and 5–6.

waves of incoming females and most of the males die close to, or on, the beach whereas females return back offshore (Templeman 1948). We interpret this behavior to indicate that males spawn more than females within a season and, consequently, are at greater risk to mortality due to greater physiological stress from multiple spawnings and/or greater physical trauma sustained in the surf zone.

Skewed sex ratios observed in fish populations have been attributed to sampling bias due to physical segregation of the sexes, to size-selective sampling, or to differential exploitation of the sexes (Hoenig and Lawing 1983; Mason and Phillips 1985; Botha 1986; Young et al. 1987). We have no evidence that sampling factors account for our results. Skewed sex ratios have also been attributed to differences in

level of predation (e.g., Clarke 1983) which is one of the factors that can lead to sex-specific life history strategies (Brown et al. 1987; Holtby and Healey 1990; Bowen et al. 1991; Mullan et al. 1992). We believe that differences in spawning behavior, more so than predation, account for the skewed sex ratio in the NAFO Div. 3L capelin stock. Whether spawning behavior has caused a sex-specific life history strategy to evolve cannot be addressed by our analyses.

Contribution of Surviving Mature Females to the Total Female Spawning Stock and Fishery

The contribution of surviving mature females to the total spawning stock could be considerable: 24–47% (excluding and including influential data points, respectively) of the

• mature spawning stock over the years 1982–90 were estimated to be mature females that had survived at least one spawning season. The contribution of older age classes may also be an important factor in regulation of capelin populations. If we assume that larval/juvenile survival is largely due to unpredictable environmental variability (Leggett et al. 1984; Frank and Leggett 1981a, 1991b), then a greater diversity of life history traits (e.g., egg size and quality, timing and/or choice of spawning location, etc.) may lead to a decreased variance in year class strength. Older females differ from younger females in various ways, such as having a greater fecundity (Nakashima 1987). Winters (1971) proposed that repeat spawners, as distinguished by otolith characteristics, had a greater fecundity than did first-time spawners of equal age and size. In essence, simply considering the number of fish may underestimate the contribution of older females to the spawning potential.

Model Adequacy

Models (1) and (2) assume interannual variability in the survival rates because the independent variables are assumed known without error in a linear regression model. Furthermore, abundance estimates act as both independent and dependent variables and are assumed known. Thus, the random error term has to refer to the variability* in survival rates. In reality, considerable measurement error probably exists in the estimates of numbers and of the proportions of mature fish. To study interannual variability in survival and survival estimates, we would need to estimate the variability in each input variable (acoustic estimates, age composition, proportion of mature fish). This has yet to be undertaken. Therefore, the estimated standard errors of our estimates of survival rates are only indicative of relative precision.

The survival estimates from the regression models are survival rates averaged over time, and these estimated averages will become more precise as more years of data are obtained. In the interim, we have developed a model for future data analyses. The present analyses with and without influential survey data points illustrate the degree of stability of the results. Certain aspects of survival are clear regardless of whether or not influential points are considered in the analysis. Thus, survival rates of immature fish appear to be comparable among the sexes, survival of mature females at ages 4 and 5 appears to be higher than that of mature males of the same age, and 4-yr-old fish appear to have higher survival than 5-yr-olds of the same sex. The greatest uncertainty concerns the survival rates of 3-yr-olds. When the influential data point is excluded, immature 3-yr-old fish have survival rates not significantly different from those of immature 2-yr-olds whereas mature fish have survival rates similar to that of mature 4-yr-olds of the corresponding sex.

We also examined interannual variability in survival rates by computing survival ratios. The observed variability in the estimates reflects both measurement error and actual interannual variability in survival. The observed variability is therefore overestimated, which is conservative. If information becomes available on the measurement errors, then we could determine if survival rates can be estimated with a given level of precision. The annual estimates of survival are imprecise as evidenced by the large fraction of estimates greater than 100%. Although we cannot obtain

precise estimates, we can still test hypotheses about the effects of age and sex. The estimate of survival for females was higher than the corresponding estimate for males at both age 4 and 5 in every year; therefore, older females have a higher survival rate than older males.

This paper provides estimates of capelin survival rates that differ from those currently being used for stock assessment in the Northwest Atlantic (see Carscadden et al. 1985) and, in the case of mature survival, those used for assessment in the Barents Sea (Tjelmeland 1985). The current NAFO Div. 3L stock assessment model, combined with the existing 10% harvest rate, has been shown to be reasonably risk averse (Shelton et al. 1993). Nevertheless, we advocate the use of the recently estimated survival rates in the future development of assessment models. The higher survival rates of mature females, and therefore the greater degree of iteroparity than previously assumed, should not be taken to imply that higher exploitation rates are acceptable. The estimates of survival rate are associated with considerable uncertainty, and this should be taken into account in an assessment procedure that quantifies the risk associated with management decisions.

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