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Factors Influencing the Rate of Sexual Maturity and the Effect on Spawning Stock for Georges Bank and Gulf of Maine Atlantic Cod *Gadus morhua* Stocks

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Abstract

Stocks of Atlantic cod, *Gadus morhua*, off the coast of New England have been heavily exploited by distant water fleets in the 1960s and 1970s and by domestic fisheries in recent years and abundance has declined. Maturation data collected by Northeast Fisheries Science Center research bottom trawl surveys from 1970–98 were examined to determine if the rate of sexual maturation of Atlantic cod varied in response to fluctuations in stock density, growth, or ambient temperature. Median age and length at maturity by sex for the 1970–96 year-classes was estimated by using logistic regression. Both age and length at maturity have significantly declined during the past 25 years. Mean length at age did not show significant trends for the time series. Stepwise logistic regression with interaction was used to determine if such factors as cod stock biomass and bottom temperature explain variation in maturation rates. Regressions were performed by aggregating all year-classes for each sex. Both stock biomass and temperature explained a significant amount of the variation ($P<0.05$) in sexual maturation. The influence of stock biomass was similar for both stocks, but bottom temperature had a slightly greater and opposite influence on maturation for Gulf of Maine cod than for Georges Bank cod. The sensitivity analysis of biological reference points to regime shifts in maturation and partial recruitment illustrated more variation in spawning stock numbers per recruit and $F_{20\%}$ than in spawning stock biomass per recruit.

Key words: Atlantic cod, biomass, Georges Bank, Gulf of Maine, maturity, temperature

Introduction

A decrease in population density results in more resources being available per individual. A consequence of less competition for resources may alter the life history of the species as described by the interaction of survival, growth, and reproduction (Gadgil and Bossert, 1970; Roff, 1984). Selective removal of phenotypes by a fishery may also lead to shifts in life history traits such as growth or size and age of sexual maturation. The seemingly dramatic changes that occur do not necessarily indicate genetic variation but rather may reflect the phenotypic plasticity for that trait (Roff, 1991; Trippel, 1995). Stearns and Crandall (1984) suggest that populations have evolved particular trajectories of age and size at maturity that reflect a genetically fixed component of growth and maturity rate and an adaptive component that responds to environmental factors. Such a shift in trajectories was observed for wild stocks of Norwegian coastal cod and Northeast Arctic cod. Under optimum laboratory conditions, observed differences in growth and maturation were determined to be influenced more by differences in the respective environments rather than by genetic variation (Godø and Moksness, 1987).

Commercially exploited fish stocks that have experienced declines in population abundance have similarly responded by altering life history traits of growth and maturation (Stearns and Crandall, 1984; Rijnsdorp 1989; Lett 1980; Beacham, 1982, 1983c; Helser and Almeida, 1997; Overholtz, 1987). Increased growth rates and earlier maturation were observed for haddock, *Melanogrammus aeglefinus* (Templeman and Bishop, 1979) and Atlantic herring, *Clupea harengus* (Sinclair *et al.*, MS 1980) when biomass declined in both stocks. In contrast, De Veen (1976) found that as growth rates of North

Sea sole, *Solea solea*, increased, the length at maturity also increased.

Shifts in growth and maturation have been observed in wide ranging stocks of commercially exploited cod from the Baltic Sea (Cardinale and Modin, 1999), the Arctic (Jorgensen, 1990), and the Barents Sea (Ponomarenko, MS 1967). In the Northwest Atlantic, declines in maturation have also been observed in recent years for Gulf of St. Lawrence cod (Beacham, 1983a), Northwest Atlantic Fisheries Organization (NAFO) Division 2J+3KL cod (Morgan and Brattey, 1997) and Div. 3Ps cod (Chen and Mello, 1999) and for the Scotian Shelf (Beacham, 1983b), Gulf of Maine (O'Brien, MS 1990; O'Brien *et al.*, 1993) and Georges Bank (O'Brien, MS 1990; O'Brien *et al.*, 1993; Hunt, 1996; Trippel *et al.*, 1997) cod stocks.

Atlantic cod, *Gadus morhua*, are assessed for management purposes by the USA as the Gulf of Maine stock and the Georges Bank stock, which includes fish from the Southern New England area (Fig. 1). The Canadian management zone for the Georges Bank stock is the Northeast Peak area of Georges Bank. During the last four decades, exploitation increased on both stocks by both distant water fleets in the 1960s and 1970s and by domestic fisheries in recent years. Stock abundance has decreased as indicated by both low survey catch rate indices and estimates of stock size from virtual population analyses (VPA). Spawning stock

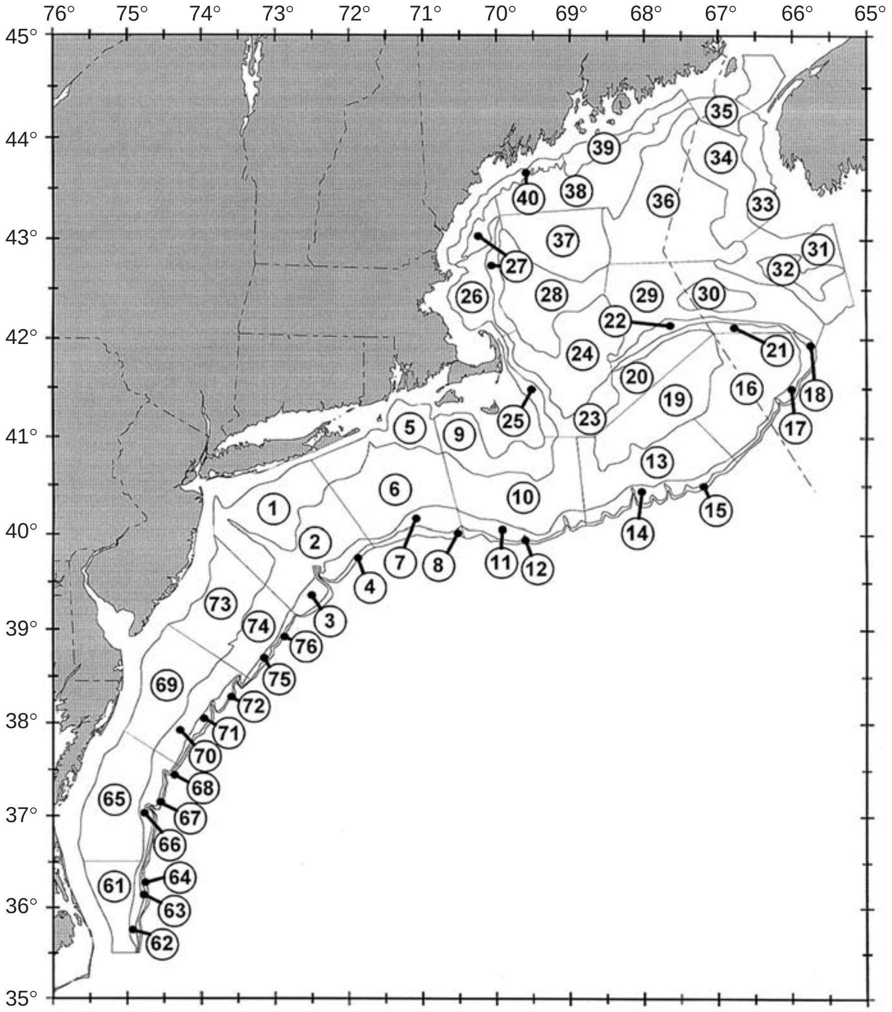

Fig. 1. NEFSC offshore bottom trawl survey strata for Southern New England (1–10), Georges Bank (13–25), and the Gulf of Maine (26–30 + 36–40). Depth range is from 27 to >200 m.

biomass (SSB) of Georges Bank cod declined 70% from 81 000 tons in 1978 to 25 000 tons in 1994 and then increased to 36 000 tons in 1997 (O'Brien and Cadrin, MS 1999). The SSB of Gulf of Maine cod declined 60% from 23 000 tons in 1982 to 9 000 tons in 1997 (Mayo *et al.*, MS 1998). The spawning season for cod is primarily from November to May with peak spawning occurring on Georges Bank during February and March and in the Gulf of Maine from March to May (Smith, MS 1985).

Observations of age at maturation of Gulf of Maine cod were first described by Earll (1880) and later by Livingstone and Dery (MS 1976) who also noted that Georges Bank cod matured at an earlier age than Gulf of Maine cod. Age and length at maturity have been described in several recent studies for both Georges Bank and the Gulf of Maine (O'Brien, MS 1990; O'Brien *et al.*, 1993; Hunt, 1996; Trippel *et al.*, 1997; Begg *et al.*, 1999).

Given the plasticity in age and length at maturity (Stearns and Crandall, 1984), it is important to monitor maturation schedules of finfish on an annual basis, particularly for heavily exploited stocks. Applying a knife edge or outdated maturation ogive in a spawning stock per recruit analysis results in biased estimates of spawning stock that influence both management decisions and interpretation of stock status. The objectives of this study are to examine trends in maturation of Georges Bank and Gulf of Maine Atlantic cod stocks during the last three decades and to determine if the variation in maturation can be explained by such factors as growth, stock density, or the environment. The effect of regime shifts in maturation on measures of stock status are then simulated for spawning stock per recruit and other biological reference points.

Methods

Data Sources

The Northeast Fisheries Science Center (NEFSC) has conducted stratified random bottom trawl surveys off the northeast coast of the USA during spring and autumn since 1968 and 1963, respectively. Details of the NEFSC bottom trawl survey procedures are described by Azarovitz (1981) and Grosslein (MS 1969, MS 1974). Length stratified sampling for age, length, and maturity stage has been conducted routinely for Atlantic cod on each survey since 1970. In this analysis, data from 1970–98 were partitioned by season into two areas, Georges Bank and the Gulf of Maine, corresponding to current Atlantic cod stock structure definitions (NEFSC offshore bottom trawl strata 13–25, and strata 26–30 plus 36–40, respectively, Fig. 1).

At sea, length measurements were recorded to the nearest cm and, for all fish sampled for age determination, the sex and maturity stage were classified through visual examination of the gonads. Maturity stage classifications were: immature, developing, ripe, ripe and running, spent, or resting (Burnett *et al.*, 1989). The age was determined from otolith readings as described by Penttila (1988).

Spring and autumn stratified mean weight per tow (kg) indices of Atlantic cod biomass were obtained from the most recent assessments of the Georges Bank (O'Brien and Cadrin, MS 1999) and the Gulf of Maine stocks (Mayo *et al.*, MS 1998). Biomass time series were fit to an autoregressive integrated moving average model (ARIMA) to obtain smoothed indices (Table 1) (Fogarty *et al.*, MS 1986; Pennington, 1985, 1986). The smoothed spring and autumn biomass indices were associated with each cohort at half-year intervals as indicators of the biomass present during the juvenile phase ranging from 0 to 2.5 years. For example, the 1970 cohort was initially produced from the survey biomass index of 17.3 kg/tow in the spring of 1970; at age 0.5 the cohort then developed as part of the 1970 autumn survey index of 12.0 kg/tow, etc., up to age 2.5 which was part of the 1972 autumn survey index of 14.9 kg/tow (Table 1).

Bottom temperature anomalies were estimated from bottom temperature data obtained during the spring and autumn NEFSC bottom trawl surveys conducted during the 1970–96 period (Holzwarth and Mountain, MS 1990; Holzwarth-Davis and Taylor, MS 1992, MS 1993, MS 1994; Taylor and Almgren, MS 1996a, MS 1996b; Taylor and Kiladis, MS 1997). A cumulative bottom temperature anomaly was associated with each cohort at half-year intervals as an indicator of whether a cohort had been exposed to warmer or cooler water during the juvenile phase. For example, the 1970 cohort on Georges Bank first appeared in the spring of 1970 when the bottom temperature anomaly was -0.7, by age 1 the cohort had been exposed to a cumulative anomaly of -2.2 (1970 spring + 1970 autumn + 1971 spring), and by age 2.5 the

TABLE 1. Spring and autumn estimated and smoothed (ARIMA) stratified mean weight per tow (kg), and spring and autumn bottom temperature anomaly (°C) for Georges Bank and Gulf of Maine Atlantic cod.

	Georges Bank Survey Biomass				Gulf of Maine Survey Biomass				Bottom Temperature Anomaly			
	Estimated		Smoothed		Estimated		Smoothed		Georges Bank		Gulf of Maine	
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
70	15.6	12.5	17.3	12.0	11.1	16.4	11.0	15.6	-0.7	-0.9	0.6	-0.2
71	14.2	9.9	18.4	13.0	7.0	16.5	9.8	14.8	-0.6	0.0	0.6	0.5
72	19.0	23.0	20.9	14.9	8.0	13.0	9.7	12.4	0.2	-0.4	0.8	0.3
73	39.7	30.8	24.4	15.6	18.8	8.7	10.1	10.0	1.0	1.0	0.6	0.7
74	36.4	8.2	25.1	14.1	7.4	9.0	8.8	9.2	1.1	0.5	1.1	1.3
75	26.0	14.1	23.7	14.3	6.0	8.6	8.1	8.7	0.6	-0.6	0.6	0.4
76	18.6	17.7	21.7	14.6	7.6	6.7	8.0	8.4	0.9	1.1	1.3	1.2
77	15.4	12.5	20.8	14.2	8.5	10.2	8.1	10.2	0.4	0.8	-0.2	0.1
78	31.2	23.3	21.3	14.2	7.7	12.9	8.1	12.3	-0.9	-0.8	-0.2	-0.4
79	16.9	16.5	20.0	12.8	9.5	17.5	8.2	14.2	-0.2	0.9	-0.2	0.4
80	16.7	6.7	19.5	11.0	6.2	14.2	7.9	12.9	0.7	0.9	0.0	-0.2
81	26.1	19.0	19.8	10.4	10.8	8.1	8.2	10.7	-0.2	-1.1	-0.3	-0.6
82	15.4	6.9	18.7	8.7	8.6	16.1	8.0	11.9	-0.3	-0.9	0.1	-0.2
83	24.0	6.5	18.6	7.6	10.5	8.8	7.5	9.6	0.7	-0.7	0.0	0.1
84	15.4	10.3	17.3	6.9	5.8	8.8	6.4	8.6	1.0	0.6	0.2	0.8
85	21.5	3.5	16.6	5.7	7.7	8.5	5.6	7.4	0.4	1.1	0.3	0.6
86	16.7	4.7	14.9	5.2	3.6	5.1	4.5	5.6	1.4	0.0	1.7	0.6
87	10.3	4.4	13.0	4.9	3.0	3.4	3.9	4.6	0.6	-1.6	0.0	-0.1
88	13.5	5.8	12.1	4.7	3.3	6.6	3.6	5.2	-0.4	-1.0	0.9	-0.4
89	10.8	4.6	10.9	4.4	2.5	4.6	3.4	4.6	0.0	-0.7	-0.2	-0.5
90	11.6	7.1	9.9	4.0	3.1	4.9	3.5	4.1	0.6	0.0	0.1	-0.2
91	9.0	1.4	8.5	3.2	2.9	2.8	3.8	3.0	0.4	0.1	0.5	0.1
92	7.5	3.1	7.3	3.1	8.7	2.5	4.4	2.3	-0.6	-0.1	0.5	0.3
93	7.3	2.2	6.2	3.0	5.9	1.0	4.3	1.7	-0.6	0.6	-0.6	-0.2
94	1.2	3.3	5.1	3.1	2.4	2.7	3.8	2.4	0.6	0.3	0.7	1.2
95	8.4	5.6	6.0	3.2	2.4	3.7	3.8	2.7	1.1	2.2	0.8	0.6
96	7.5	2.7	6.5	2.9	5.4	2.4	4.2	2.3	-0.2	-2.1	0.7	-0.6
97	5.2	1.9	6.8	2.7	5.6	1.9	4.5	1.9	-0.1	0.3	1.3	0.5
98	11.7	2.8	7.5	2.7	4.2	1.5	4.4	1.7	0.4	-0.8	1.1	-0.3

cumulative anomaly was -2.4 (Table 1). Missing temperature data were recorded as a zero anomaly.

Maturity Analysis

Proportions mature at age and length for the 1970–96 year-classes were derived for each stock by sex using spring maturity observations. Individual maturity observations were re-coded as either immature or mature. The mature category included all fish identified as developing, ripe, ripe and running, or resting. A linear logistic regression model was fit to the observed proportions mature (p) by the method of maximum likelihood with the logit link function (SAS, 1990). The form of the logistic model is:

$$\text{logit}\,(p) = \log\left(\frac{p}{1-p}\right) \qquad (1)$$

where

$$p = \frac{1}{1+e^{-(\alpha+\beta x)}} \qquad (2)$$

Median maturity, defined as the age or length at which 50% of the fish are mature (A_{50} and L_{50}, respectively), was derived from the regression coefficients as $-(\alpha/\beta)$.

Prior to fitting the logistic, the observed proportions mature at age for each year were weighted by the abundance at length (Anon., MS 1994; Morgan and Hoenig, 1997) and the proportions mature at length were used directly as estimated from the observed data. The abundance was applied for an entire strata set rather than by single individual strata as recommended by

Morgan and Hoenig (1997) because preliminary examination of mean length of cod within each stratum indicated no patterns in the distribution of cod by length among stratum over the time series. The stratified mean abundance at length for the total strata set for Georges Bank and Gulf of Maine was then applied as the weighting factor for proportion mature at age by:

$$M'_a = \frac{\sum_{j=1}^{J} P'_j P'_{a|j} P'_{m|aj}}{\sum_{j=1}^{J} P'_j P'_{a|j}} \qquad (3)$$

where: P'_j = estimated proportion of the catch at length j,
$P'_{a|j}$ = proportion of sampled fish at length j that are age a,
$P'_{m|aj}$ = proportion of sampled fish at age a which are mature at length j.

The weighted proportions mature at age were rescaled by the total number observed at length and age to allow for testing of significance of fit to the model. The null hypothesis that the logistic model fits the proportion of mature cod at length or age was evaluated using maximum likelihood estimation with a chi-square test for significance of the covariates (SAS, 1990). All non-significant estimates (P>0.05) were excluded from further analyses. The variance of L_{50} and A_{50} was calculated using an analytical approximation for large samples (Ashton, 1972) as:

$$s^2(y) = \frac{1}{b^2}\left[s^2(a) + \frac{a^2}{b^2}s^2(b) - \frac{2a}{b}cov\ (a,b)\right] \qquad (4)$$

The computational equation for this formula is:

$$s^2(y) = \frac{1}{b^2}\left[s^2(a') + (y-\bar{x})^2 s^2(b)\right] \qquad (5)$$

where: a, b = estimates of α and β
y = length or age at maturity for a given proportion
$s^2(a')$ = $1/\sum nPQ$
$\bar{x}$ = $\sum nPQx / \sum nPQ$
P = probability of a response
Q = $1 - P$
n = number of fish at length or age x
$s^2(b)$ = variance of b.

Approximate 95% confidence limits were calculated for L_{50} and A_{50} because exact confidence limits for the statistic y are not available (Sokal and Rohlf, 1981). The t-distribution was used at an alpha level of 0.05 for varying degrees of freedom (df) with the standard error of y as: $y \pm t_{0.05,df}\, s(y)$.

Linear regressions of L_{50} and A_{50} were conducted to test for significant trends in maturation over time for the 1970–96 year-classes. In addition, maturation ogives were generated for each year-class and the time series of estimated percent mature at age was regressed against time to test for significant trends. Residuals (observed-predicted) of proportion mature at age were calculated for ages 1 through 6 for both stocks.

Model Development

Stepwise logistic regression with interactions was used to develop a model to describe variation in the proportion mature at length. The logistic model from equation 1 can be written in linear form with interaction terms as:

$$\log\frac{p}{1-p} = \beta_o + B_1X_1 + B_2X_2 + B_3X_1X_2 .... B_nX_n \qquad (6)$$

The response variable was proportion mature at length for all observations from the 1970–96 year-classes. The explanatory variables were area, sex, length (cm), cod stock biomass (kg/tow), and the bottom temperature anomaly (°C). The interaction terms were area×biomass, area×temperature, area×sex, area×length, sex×length, and area×sex ×length. Age was not considered as an explanatory variable because the correlation of age with length would confound the results.

Initially, a series of 36 exploratory models were formulated by forcing the main explanatory variables of area, sex, length, one biomass variable, e.g. biomass at age 0.5, and one cumulative bottom temperature anomaly variable, e.g., at age 0. The interaction terms were allowed to enter the model by forward stepwise selection. Candidate models were chosen based on the lowest Akaike Information Criterion (AIC) which indicates the best fitting model (SAS, 1990). The criteria for acceptance of the null hypothesis, that all independent variables are equal, was a significance level of 0.05.

Using the final model, predictions of proportion mature at length were simulated over the range of observed cod biomass indices and bottom temperature anomalies for both Georges Bank and Gulf of Maine for both sexes. For Georges Bank, the survey biomass index ranged from 5 to 25 kg/tow and the bottom temperature anomaly ranged from -0.9 to 1.4°C. Similarly, for the Gulf of Maine predictions, the survey biomass index ranged from 3 to 11 kg/tow and the bottom temperature anomaly ranged from -0.63 to 1.7°C (Table 1). In addition, the proportion mature at length for a 45 cm and 33 cm fish from Georges Bank and the Gulf of Maine, respectively, was simulated for both sexes under conditions of low and high biomass and bottom temperature anomaly. The low and high estimates were derived from the 25th and 75th percentile, respectively, of the Gulf of Maine biomass indices and bottom temperature anomalies.

Growth analysis

Analysis of covariance was used to test the null hypotheses of equal slopes (β) and equal *y*-intercepts (α) between sexes for each year-class to determine if mean lengths, adjusted for age, were similar between sexes (Sokal and Rohlf, 1981). Empirical length-at-age data, obtained in April and October in most years, were combined by season, and ages were adjusted to account for the month of sample collection. The aging convention assumes a birth date of 1 January for Atlantic cod (Penttila *et al.*, 1988); therefore, 0.3 and 0.8 years were added to the spring and autumn ages, respectively. The form of the covariance model used was:

$$Y_{ij} = \mu + \alpha_i + \beta_{within}\left(X_{ij} - \overline{X}_i\right) + \varepsilon_{ij} \tag{7}$$

where:

Y_{ij} = length of *j*th observation for sex_i (i = 1,2) or $year\text{-}class_i$ (i = 70, 71...96),

μ = grand mean of the population,

α_i = fixed treatment effect for sex_i or $year\text{-}class_i$,

β_{within} = slope of the pooled regression within groups,

X_{ij} = $ln(age)$; covariate,

$X_{ij} - \overline{X}_i$ = effect explained by the difference of the variate X_{ij} from the $\overline{X}_i$

ε_{ij} = random deviation.

Linear regressions of length-at-age data were performed to detect significant trends in growth over the time series. Length-at-age data as described above were further aggregated into two year blocks, and the mean length-at-age was estimated and regressed against time to test the null hypothesis of a slope equal to zero.

Length-at-age data for ages 2–4 for both sexes, by season, was also examined graphically using Tukey's box plots (Cleveland, 1993). The data plotted are the median length, first and third quartiles, ranges, outliers, and the 95% confidence interval of the median. In addition, a locally weighted regression (loess) smooth (SPLUS, 1997) of the mean length (span = 0.2), and a loess smooth of the bottom temperature anomaly (span = 0.3) were overlaid on the Tukey box plots.

Spawning Stock per Recruit Sensitivity Analysis

Spawning stock per recruit analysis was performed to determine the sensitivity of spawning stock estimates to shifts in both the maturation ogive and partial recruitment. Spawning stock biomass per recruit was calculated for a cohort (Gabriel *et al.*, 1989) as:

$$\sum SSB_i = N_i \cdot PM_i \cdot MW_i \tag{8}$$

where:

i = age 1, 2, ...10+

N = $N_{i-1} \cdot e^{-Z(i-1)}$,

Z = $\left(F \cdot PR_i\right) + M$,

F = fishing mortality,

M = natural mortality = 0.2,

PR_i = partial recruitment; fishing mortality at age i,

PM_i = proportion of fish mature at age i,

MW_i = mean weight at age i.

Total spawning stock per recruit in numbers $(N_i \cdot PM_i)$ was also estimated. Mean weights at age were kept constant for all scenarios using current population weights since no trends have been observed throughout the time series (O'Brien and Cadrin, MS 1999). Partial recruitment, the proportion of fully recruited *F* that is applied to fish ages 1–3, was calculated by dividing each age specific *F* by the mean *F* at fully recruited fish ages 4–8, obtained from VPA (O'Brien and Cadrin, MS 1999). Each simulation was conducted for fishing mortalities ranging from 0.1 to 1.0.

Spawning stock per recruit was simulated for four scenarios: 1) early *PR* with early maturation (A_{50} is at a younger age), 2) delayed *PR* with late maturation (A_{50} is at an older age), 3) early *PR* with late maturation, and 4) delayed *PR* and early maturation. The early and delayed *PR* vectors were from 1982 (age 1: 0.03, age 2: 0.51, age 3: 0.75, age 4: 1.00) and 1994 (age 1: 0.00, age 2: 0.06, age 3: 0.58, age 4: 1.00), respectively (O'Brien and Cadrin, MS 1999). The early and late maturation schedules were derived from the logistic regression of females from the 1987 and 1971 Georges Bank year-classes, respectively, as described above in the maturity analysis section.

Results

Graphical comparisons of weighted *vs* unweighted proportions mature at age (not presented here) generally indicated very little difference between the methods. Unweighted A_{50} and weighted A_{50} estimates in each of the four sets of analyses were different from each other by more than 0.5 years for only about 4%–11% of the 27 year time series. These results are similar to the conclusions of Morgan and Hoenig (1997) for both cod and American plaice. Despite this, the weighted proportions mature at age, re-scaled to counts, were used in all subsequent analyses.

The null hypothesis that the logistic model fits the proportion of mature cod at length or age was accepted ($P<0.05$) for the majority of the Georges Bank and Gulf of Maine year-classes. Median maturity at age for Georges Bank cod was about one year earlier than the Gulf of Maine cod. Georges Bank females and males had an average A_{50} of 2.1 years, ranging from ages 1.3 to 3.3 and the Gulf of Maine females and males had an average A_{50} of 2.9 years, ranging from ages 1.8 to 4.2 (Fig. 2a and 2b).

Average median length at maturity was similar between the stocks with the Gulf of Maine stock exhibiting a wider range of L_{50} values. Georges Bank females and males had an average L_{50} of 45.2 cm, ranging from 31.3 cm to 57.0 cm and the Gulf of Maine females and males had an average L_{50} of 42.0 cm, ranging from 27.9 cm to 71.7 cm.

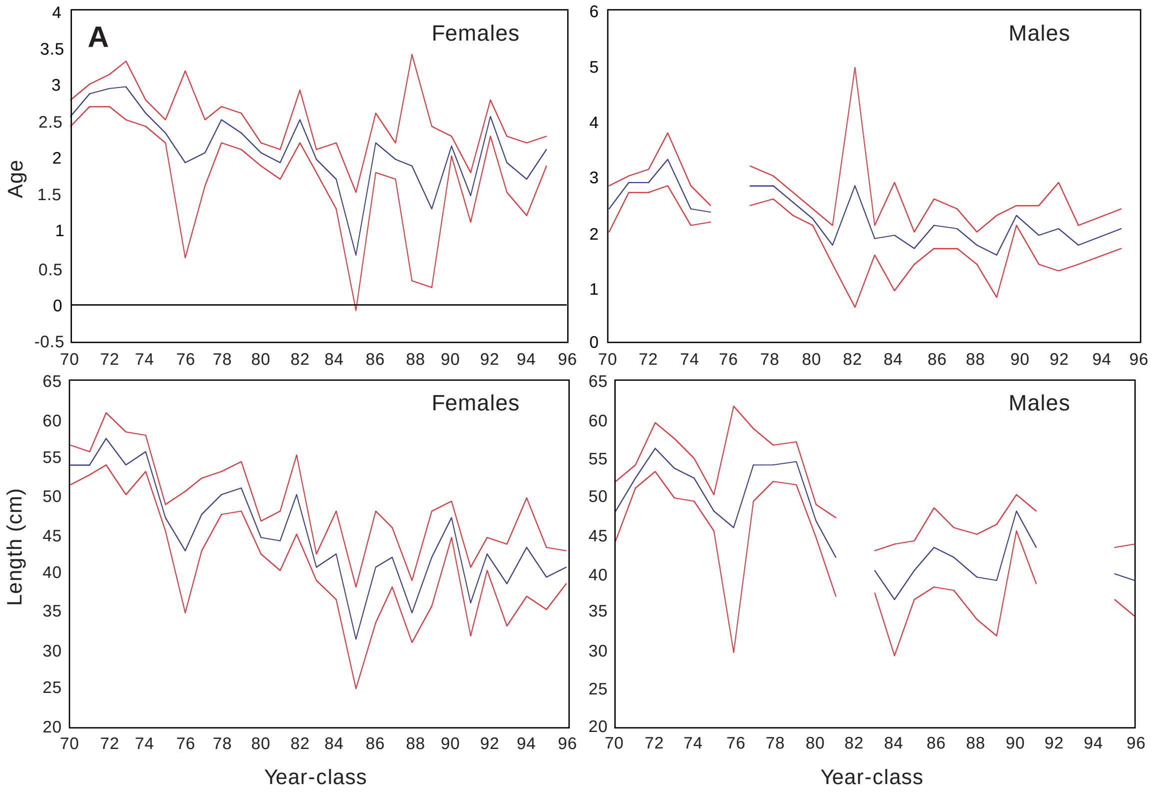

Fig. 2a. Median age and length at maturity (blue line) with 95% confidence intervals (red line) for (**A**) Georges Bank and (**B**) Gulf of Maine Atlantic cod year-classes, 1970–96.

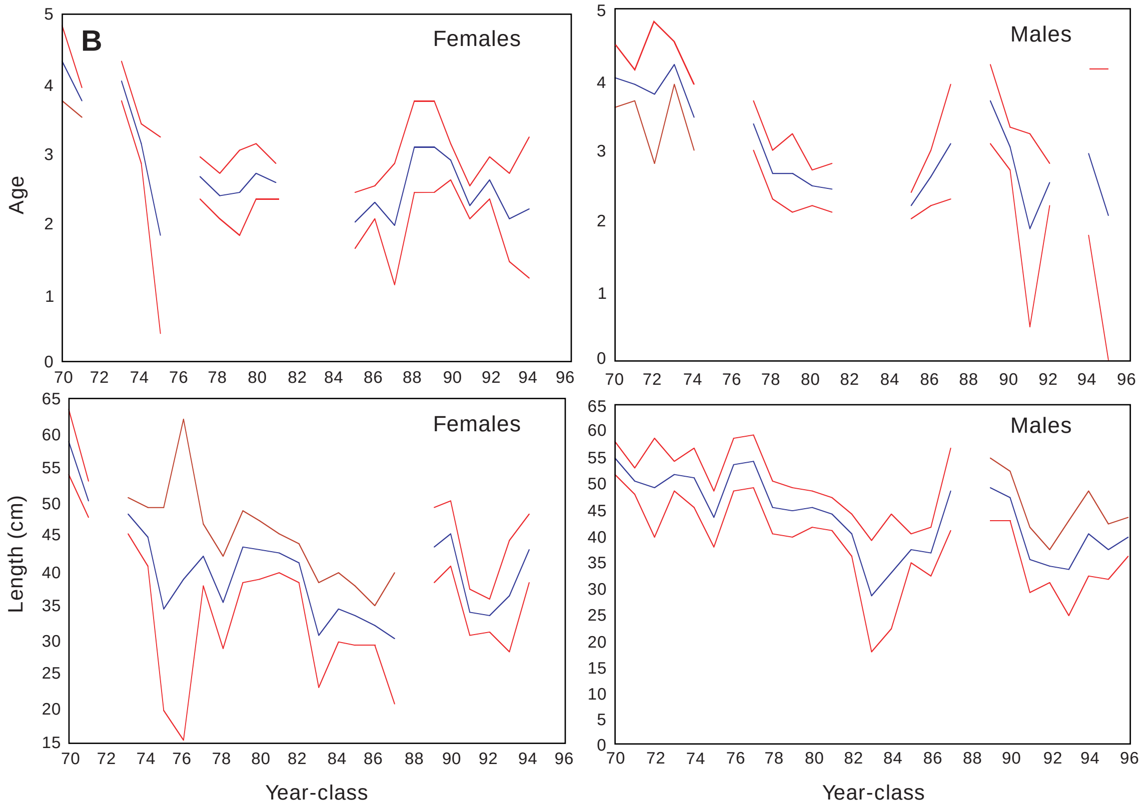

Fig. 2b. Median age and length at maturity (blue line) with 95% confidence intervals (red line) for (**A**) Georges Bank and (**B**) Gulf of Maine Atlantic cod year-classes, 1970–96.

The age at 100% maturity, although variable, has generally declined by one year throughout the time series for both areas (Tables 2a and 2b). On Georges Bank, 100% maturity occurred between ages 5 and 6 early in the time series and in the more recent year-classes has shifted to ages 4 and 5 for both sexes. Similarly, in the Gulf of Maine, 100% maturity was attained between ages 6 and 7 in the earlier year-classes and has shifted to ages 5 and 6 in the recent year-classes for both sexes.

Linear regressions of L_{50} and A_{50} year-class values against time indicated significant departures ($P<0.05$) from the null hypothesis of zero slope in all cases for both Georges Bank and Gulf of Maine females and males (Fig. 2a and 2b). The difference in the average maturation between the first and last 5 year-classes indicated a decline in A_{50} of about 0.8 years and 1.4 years for Georges Bank and the Gulf of Maine, respectively. The decline in L_{50} was about 13 cm for both stocks.

Linear regression analysis of estimated proportion mature at age against the time series showed significant differences from a slope of zero ($P<0.05$) for ages 2 to 5 for both stocks. The proportion mature at ages 2 through 4 significantly increased over the time series for both sexes on Georges Bank. In the Gulf of Maine, the proportion mature increased significantly over the time series for females from ages 3 through 5 and for males from ages 2 through 4 (Tables 2a and 2b, and Fig. 3).

The examination of residuals for all year-classes by area, age, and sex reflected the lack of samples in the youngest and oldest ages. Residuals were generally negative for age 1, positive for age 2, variable for ages 3, 4, and 5, and positive for age 6. While the pattern in the residuals may be problematic for the tails of the logistic distribution, the expected effect on the estimation of median maturity would not be significant.

Model Development

All exploratory models are presented in the order in which significant interaction terms were added to the forced main effects (area, sex, length, biomass, bottom temperature anomaly) by the stepwise regression (Table 3). In all models, each additional interaction term lowered the AIC. Neither the interaction term sex×length nor area×sex was significant in any of the exploratory models.

The final model with the lowest AIC that best explained variation in maturation included the explanatory variables of stock area, sex, length, cod biomass at age 1.5, cumulative bottom temperature anomaly at age 1.0, and the interaction terms of area×bottom temperature anomaly, area×length, and area×sex×length:

$$\mathit{logit}\,(p) = -5.8594 + 1.7778 * \mathrm{Area} - 0.1003 * \mathrm{Sex} + 0.1621 * \mathrm{Length} - 0.1730 * \mathrm{Biomass} + 0.0595 * \mathrm{Temperature} - 0.2467 * \mathrm{Area} \times \mathrm{Temperature} - 0.0223 * \mathrm{Area} \times \mathrm{Length} - 0.00855 * \mathrm{Area} \times \mathrm{Sex} \times \mathrm{Length}.$$

The model results indicate that the length at which maturation occurs is mediated by the cod stock biomass and bottom temperature during the juvenile phase between age 1 and age 1.5.

Simulations of proportion mature at length for a range of biomass indices at both a low (cool) and

TABLE 2a. Predicted proportion mature at ages 1–5, median maturity at age (A_{50}), and total number of fish observed (ages 1–14+) for Georges Bank and Gulf of Maine Atlantic cod 1970–96 year-classes. Dash indicates lack of fit to the model (P>0.05).

	Georges Bank													
	Females							Males						
Year-class	Age 1	2	3	4	5	A_{50}	Total number	Age 1	2	3	4	5	A_{50}	Total number
70	0.03	0.23	0.72	0.96	0.99	2.6	143	0.16	0.38	0.68	0.87	0.96	2.4	104
71	0.00	0.07	0.61	0.97	1.00	2.9	503	0.02	0.14	0.56	0.90	0.99	2.9	429
72	0.01	0.10	0.54	0.93	0.99	2.9	142	0.01	0.11	0.57	0.93	0.99	2.9	139
73	0.05	0.19	0.52	0.84	0.96	2.9	90	0.03	0.13	0.38	0.73	0.92	3.3	74
74	0.01	0.13	0.76	0.99	1.00	2.6	142	0.10	0.33	0.70	0.92	0.98	2.4	129
75	0.04	0.30	0.83	0.98	1.00	2.4	396	0.03	0.27	0.84	0.99	1.00	2.4	340
76	–	–	–	–	–	–	27	–	–	–	–	–	–	27
77	0.26	0.48	0.70	0.86	0.94	2.1	188	0.13	0.30	0.54	0.77	0.90	2.8	186
78	0.07	0.30	0.71	0.93	0.99	2.5	159	0.01	0.12	0.60	0.94	0.99	2.8	156
79	0.04	0.31	0.83	0.98	1.00	2.3	108	0.00	0.13	0.85	1.00	1.00	2.5	90
80	0.08	0.47	0.89	0.99	1.00	2.1	288	0.02	0.33	0.91	0.99	1.00	2.2	293
81	0.04	0.57	0.97	1.00	1.00	1.9	138	0.20	0.61	0.91	0.98	1.00	1.8	130
82	0.04	0.25	0.72	0.95	0.99	2.5	72	–	–	–	–	–	–	49
83	0.03	0.54	0.98	1.00	1.00	2.0	212	0.16	0.57	0.90	0.98	1.00	1.9	224
84	0.18	0.65	0.94	0.99	1.00	1.7	76	–	–	–	–	–	–	57
85	–	–	–	–	–	–	294	0.27	0.60	0.86	0.96	0.99	1.7	285
86	0.08	0.40	0.83	0.97	1.00	2.2	88	0.12	0.45	0.82	0.96	0.99	2.1	94
87	0.19	0.52	0.83	0.96	0.99	2.0	157	0.21	0.48	0.75	0.91	0.97	2.1	183
88	–	–	–	–	–	–	86	0.17	0.64	0.94	0.99	1.00	1.7	81
89	0.42	0.69	0.87	0.95	0.98	1.3	54	0.36	0.62	0.83	0.93	0.98	1.6	64
90	0.01	0.33	0.98	1.00	1.00	2.2	155	0.02	0.29	0.91	1.00	1.00	2.3	150
91	0.19	0.84	0.99	1.00	1.00	1.5	47	0.14	0.53	0.88	0.98	1.00	1.9	60
92	0.00	0.03	0.94	1.00	1.00	2.5	105	–	–	–	–	–	–	103
93	0.10	0.56	0.94	0.99	1.00	1.9	78	0.13	0.65	0.96	1.00	1.00	1.8	91
94	0.12	0.68	0.97	1.00		1.7	41	–	–	–	–	–	–	39
95	0.02	0.40	0.97			2.1	56	0.07	0.47	0.91			2.1	52
96	–	–	–	–	–	–	34	–	–	–	–	–	–	26

TABLE 2b. Predicted proportion mature at ages 1–5, median maturity at age (A_{50}), and total number of fish observed (ages 1–14+) for Georges Bank and Gulf of Maine Atlantic cod 1970–96 year-classes. Dash indicates lack of fit to the model (P>0.05).

	Gulf of Maine													
	Females							Males						
Year-class	Age 1	2	3	4	5	A_{50}	Total number	Age 1	2	3	4	5	A_{50}	Total number
70	0.01	0.04	0.15	0.41	0.74	4.3	53	0.01	0.04	0.17	0.49	0.81	4.0	60
71	0.00	0.02	0.17	0.65	0.94	3.7	237	0.00	0.02	0.14	0.55	0.90	3.9	230
72	–	–	–	–	–	–	34	0.04	0.11	0.28	0.56	0.81	3.8	25
73	0.01	0.04	0.17	0.49	0.82	4.0	191	0.01	0.03	0.14	0.43	0.78	4.2	150
74	0.00	0.03	0.43	0.95	1.00	3.1	76	0.00	0.00	0.13	0.90	1.00	3.5	46
75	0.26	0.57	0.83	0.95	0.98	1.8	48	–	–	–	–	–	–	37
76	–	–	–	–	–	–	31	–	–	–	–	–	–	18
77	0.04	0.22	0.67	0.94	0.99	2.6	109	0.03	0.11	0.37	0.74	0.93	3.3	101
78	0.01	0.23	0.90	1.00	1.00	2.4	58	0.04	0.23	0.65	0.92	0.99	2.7	77
79	0.16	0.39	0.67	0.87	0.96	2.4	49	0.08	0.27	0.62	0.87	0.97	2.7	42
80	0.05	0.24	0.64	0.91	0.98	2.7	84	0.01	0.18	0.83	0.99	1.00	2.5	76
81	0.00	0.12	0.83	0.99	1.00	2.6	77	0.00	0.11	0.92	1.00	1.00	2.5	39
82	–	–	–	–	–	–	61	–	–	–	–	–	–	46
83	–	–	–	–	–	–	52	–	–	–	–	–	–	47
84	–	–	–	–	–	–	29	–	–	–	–	–	–	39
85	0.17	0.51	0.84	0.96	0.99	2.0	81	0.04	0.36	0.89	0.99	1.00	2.2	96
86	0.00	0.19	0.98	1.00	1.00	2.3	69	0.06	0.26	0.66	0.91	0.98	2.6	77
87	0.34	0.51	0.67	0.81	0.89	2.0	155	0.26	0.37	0.49	0.62	0.73	3.1	143
88	0.02	0.12	0.47	0.86	0.98	3.1	21	–	–	–	–	–	–	25
89	0.02	0.12	0.47	0.86	0.98	3.1	22	0.00	0.02	0.17	0.68	0.96	3.7	22
90	0.00	0.04	0.61	0.98	1.00	2.9	42	0.00	0.00	0.43	1.00	1.00	3.0	43
91	0.01	0.28	0.96	1.00	1.00	2.2	63	0.25	0.55	0.81	0.94	0.98	1.9	48
92	0.00	0.09	0.83	1.00	1.00	2.6	114	0.03	0.23	0.76	0.97	1.00	2.5	107
93	0.05	0.48	0.94	1.00	1.00	2.0	26	–	–	–	–	–	–	34
94	0.10	0.42	0.82	0.97		2.2	33	–	–	–	–	–	–	35
95	–	–	–	–	–	–	10	–	–	–	–	–	–	23
96	–	–	–	–	–	–	14	–	–	–	–	–	–	13

high (warm) bottom temperature anomaly demonstrate the influence of biomass and temperature on the rate of maturation for both stocks (Fig. 4a and 4b). Georges Bank cod mature at a faster rate than the Gulf of Maine cod, under any condition of biomass or temperature. The proportions mature at length for Gulf of Maine cod are influenced slightly more by temperature and in the opposite direction than that for Georges Bank cod. For example, for an age 2 female cod from Georges Bank that is 45 cm, the difference in proportion mature at length between warm and cool temperature is +1% at low biomass. In contrast, for an age 2 female cod from the Gulf of Maine that is 33 cm the difference is -3.6% at low biomass (Table 4).

Growth analysis

The growth rate of female and male cod, adjusted for age, was not significantly different from each other for the majority of the year-classes for both stocks. Two-thirds of the Georges Bank year-classes appear to have similar growth rates between females and males. The null hypothesis of equal slopes, i.e. no interaction of the treatment (sex) and the covariate (age) was rejected for 7 of the 27 Georges Bank year-classes and of the remaining 20, the null hypothesis of equal intercepts was rejected for 2 year-classes (Table 5). Seventy-five percent of the Gulf of Maine year-classes have similar growth rates between females and males. The null hypothesis of equal slopes was rejected

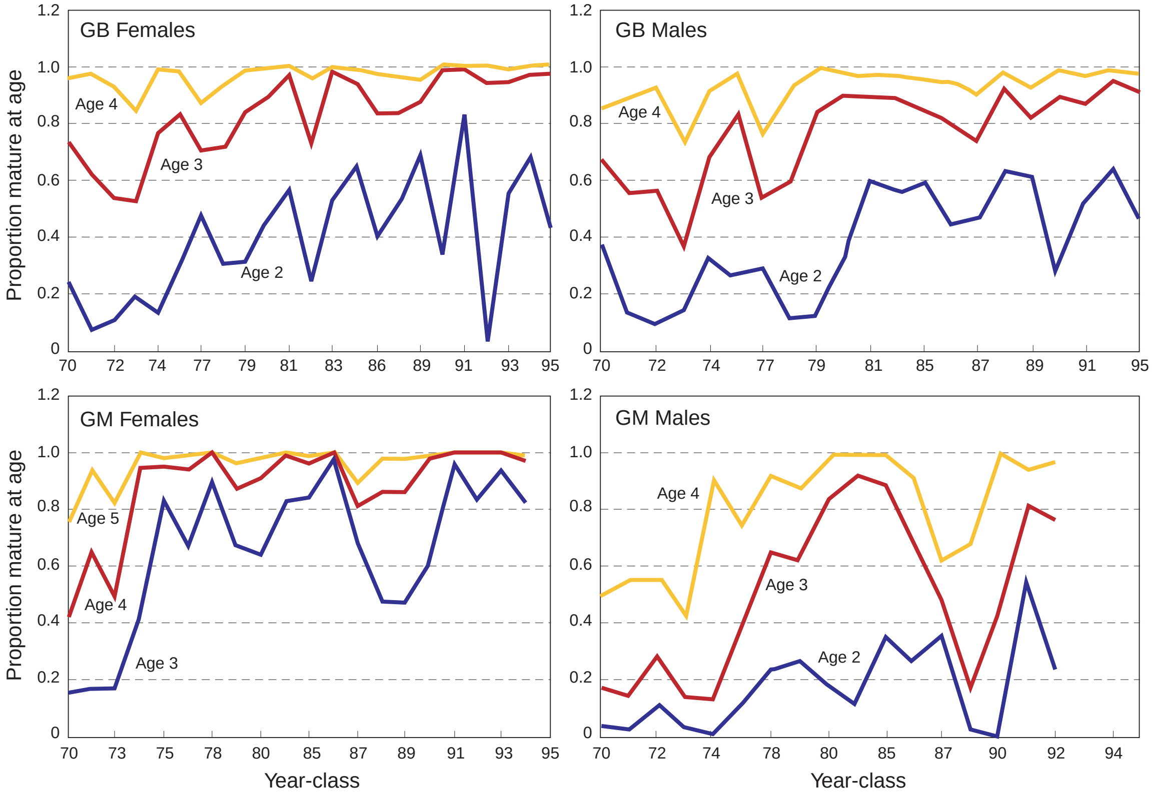

Fig. 3. Estimated proportion mature at age for females and males, ages 2–4, for Georges Bank (GB) and Gulf of Maine (GM) Atlantic cod 1970–95 year-classes.

for 3 of the 27 Gulf of Maine year-classes, and of the remaining 24, the null hypothesis of equal intercepts was rejected for 4 year-classes (Table 5).

Although the difference was not significant for most year-classes, females generally grew slightly faster than males as indicated by a larger slope for both stocks. In the Gulf of Maine, the more recent year-classes indicate that the males grew faster than the females (Table 5).

Mean length-at-age has not significantly increased or decreased for either female or male cod from Georges Bank or the Gulf of Maine. Linear regression of empirical mean length at ages 1–8 aggregated by two year blocks indicated no significant departure (P<0.05) from a slope of zero for females or males in either stock.

Median length for ages 2–4 did not indicate strong trends over time, by season, but the stocks did exhibit periods of increase and decrease in the median lengths (Fig. 5a–5d). Median length for Georges Bank fish in the spring appears variable over the time period except for age 3 fish. For both sexes at age 3, median length appears to be declining since the mid-1980s. The autumn median lengths (Fig. 5b) show a similar pattern of variability, except for age 3 males which appear to be increasing in the mid-1990s. The sample size for these latter years is smaller, however. In the Gulf of Maine, median lengths for both sexes in both seasons all have a similar pattern of increasing length in the late-1970s, a peak about 1980 and then decreasing length in the mid- 1980s (Fig. 5c–5d). Median length appears to be increasing after 1990 for ages 2 and 3 for both sexes, except for age 3 females in the autumn.

Spawning Stock per Recruit Sensitivity Analysis

The spawning stock per recruit sensitivity analysis indicated that shifts in PR and maturation rate influence spawning stock numbers per recruit (SSN/R) more than stock biomass per recruit (SSB/R). For example, at F = 0.2, earlier maturation can produce between 20% to 55% more SSN/R than

TABLE 3. AIC scores for all exploratory stepwise logistic models. The first column of AIC scores represents the base model results with forced effects of area, sex, length (len), biomass (bio) at ages ranging from 0 to 2.5, and cumulative bottom temperature anomaly (temp) associated with ages 0 to 2.5. In columns 2–5, the interaction terms are denoted by concatenating the main effects, i.e. area × biomass is presented as areabio. In each row, each interaction model includes the base model and all previous interaction terms reading from left to right. The digits after bio and temp are the age associated with that factor, i.e., bio 1.5 is the survey biomass (kg/tow) at age 1.5 and temp 0.5 is the cumulative bottom temperature anomaly (°C) associated with age 0.5. The final model with the lowest AIC is bolded (biomass 1.5 and temp 1.0 with interaction terms areatemp, arealen, and areasexlen).

Base Models		Interaction Models			
Bio 0	temp 0	areabio	areatemp	areasexlen	arealen
	7498.5	7427.0	7405.2	7387.6	7382.0
	temp 0.5	areabio	areasexlen	arealen	
	7561.0	7484.9	7467.6	7464.6	
	temp 1.0	areabio	areasexlen	areatemp	arealen
	7552.2	7475.2	7458.0	7448.4	7444.4
	temp 1.5	areabio	areasexlen	areatemp	arealen
	7553.5	7471.0	7453.7	7450.9	7447.6
	temp 2.0	areabio	areasexlen	arealen	areatemp
	7563.4	7480.5	7463.0	7460.6	7458.7
	temp 2.5	areabio	areasexlen	arealen	
	7582.7	7502.5	7484.9	7481.8	
Bio 0.5	temp 0	arealen	areatemp	areasexlen	
	7308.2	7290.4	7274.4	7266.6	
	temp 0.5	arealen	areasexlen	areatemp	
	7319.2	7301.3	7293.1	7290.5	
	temp 1.0	arealen	areatemp	areasexlen	
	7319.6	7301.7	7287.5	7279.4	
	temp 1.5	arealen	areatemp	areasexlen	areabio
	7315.9	7298.5	7284.2	7276.0	7274.0
	temp 2.0	arealen	areatemp	areasexlen	areabio
	7317.7	7300.3	7288.3	7280.1	7277.3
	temp 2.5	arealen	areasexlen	areatemp	areabio
	7320.1	7302.3	7294.1	7287.4	7283.3
Bio 1.0	temp 0	areabio	areatemp	areasexlen	arealen
	7391.0	7322.3	7305.3	7288.0	7282.0
	temp 0.5	areabio	areasexlen	arealen	
	7420.1	7352.2	7335.0	7330.7	
	temp 1.0	areabio	areasexlen	areatemp	arealen
	7416.9	7349.2	7332.1	7316.4	7311.2
	temp 1.5	areabio	areasexlen	areatemp	arealen
	7419.6	7348.8	7331.7	7323.8	7319.1
	temp 2.0	areabio	areasexlen	areatemp	arealen
	`7420.821	7350.3	7333.0	7324.9	7320.3
	temp 2.5	areabio	areasexlen	arealen	
	7431.5	7361.2	7343.8	7339.6	
Bio 1.5	temp 0	arealen	areatemp	areasexlen	
	7275.9	7257.6	7237.0	7229.0	
	temp 0.5	arealen	areasexlen	areatemp	
	7278.3	7259.6	7251.2	7244.3	
	temp 1.0	**areatemp**	**arealen**	**areasexlen**	
	7278.3	7256.9	7236.2	**7228.0**	
	temp 1.5	areatemp	arealen	areasexlen	
	7277.9	7257.4	7238.3	7230.0	
	temp 2.0	areatemp	arealen	areasexlen	
	7278.0	7256.1	7237.4	7229.3	
	temp 2.5	areatemp	arealen	areasexlen	
	7277.8	7255.3	7237.4	7229.2	
Bio 2.0	temp 0	areabio	areasexlen	areatemp	arealen
	7349.8	7259.9	7243.5	7239.8	7236.1
	temp 0.5	areabio	areasexlen	arealen	
	7355.4	7268.2	7251.6	7248.2	
	temp 1.0	areabio	areasexlen	areatemp	arealen
	7353.8	7266.3	7249.8	7244.0	7240.4
	temp 1.5	areabio	areasexlen	arealen	areatemp
	7353.8	7265.3	7248.7	7245.7	7243.2
	temp 2.0	areabio	areasexlen	areatemp	arealen
	7351.5	7262.9	7246.3	7242.6	7239.3
	temp 2.5	areabio	areasexlen	arealen	
	7354.0	7265.8	7249.2	7246.0	
Bio 2.5	temp 0	arealen	areatemp	areasexlen	
	7303.0	7283.9	7272.2	7264.1	
	temp 0.5	arealen	areasexlen	areatemp	
	7303.0	7283.6	7275.4	7273.0	
	temp 1.0	arealen	areatemp	areasexlen	
	7302.6	7282.8	7260.5	7252.3	
	temp 1.5	areatemp	arealen	areasexlen	
	7303.4	7282.5	7262.1	7253.9	
	temp 2.0	areatemp	arealen	areasexlen	
	7303.4	7279.1	7258.9	7250.9	
	temp 2.5	areatemp	arealen	areasexlen	
	7303.4	7277.5	7258.0	7249.9	

later maturation, depending on the partial recruitment (Fig. 6). Similarly, earlier maturation can produce between 3% less or 19% more *SSB/R* than later maturation (Fig. 6).

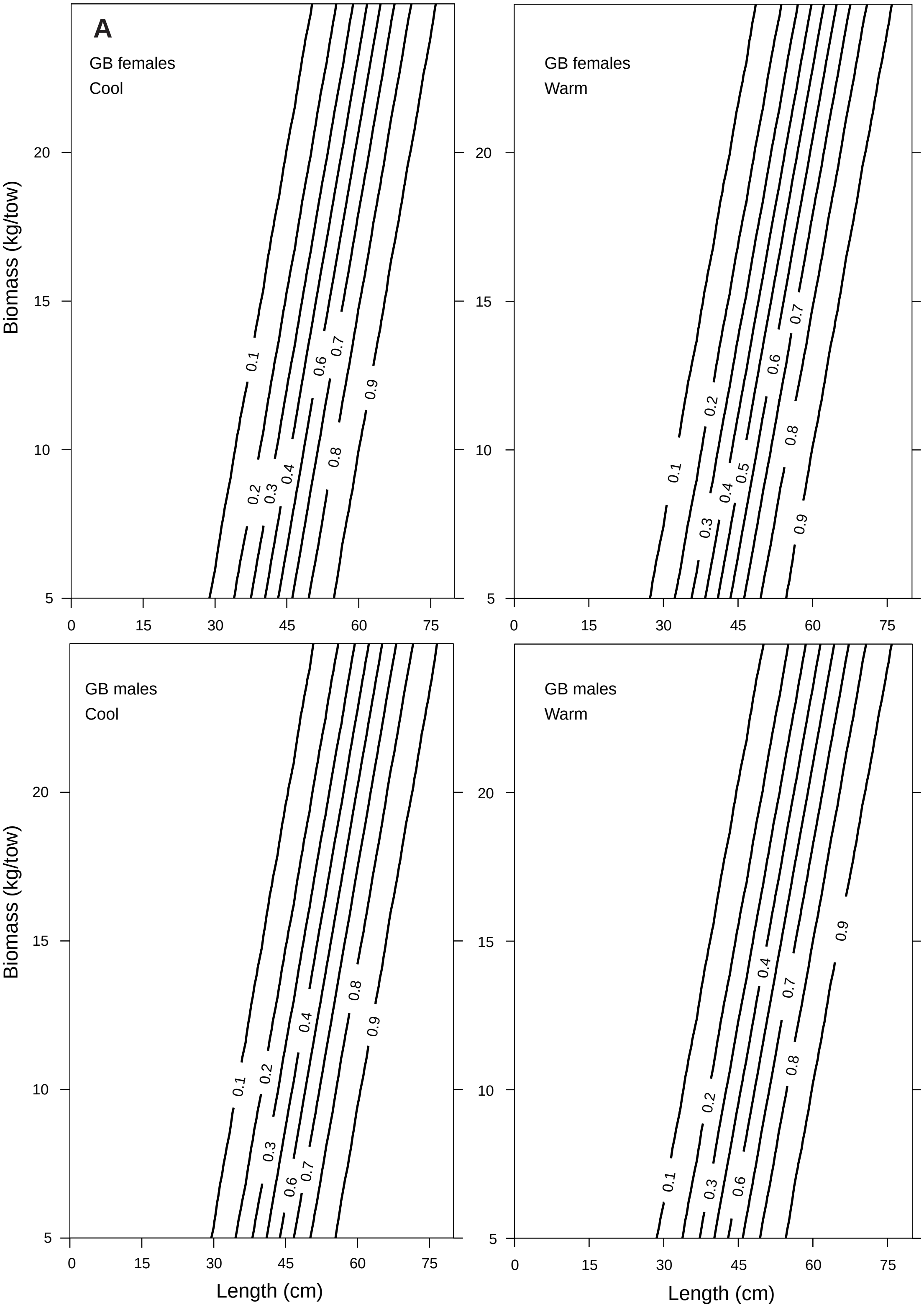

Fig. 4a. Simulated proportions mature at length for a range of biomasses at a cool and warm temperature for female and male Georges Bank (GB) Atlantic cod.

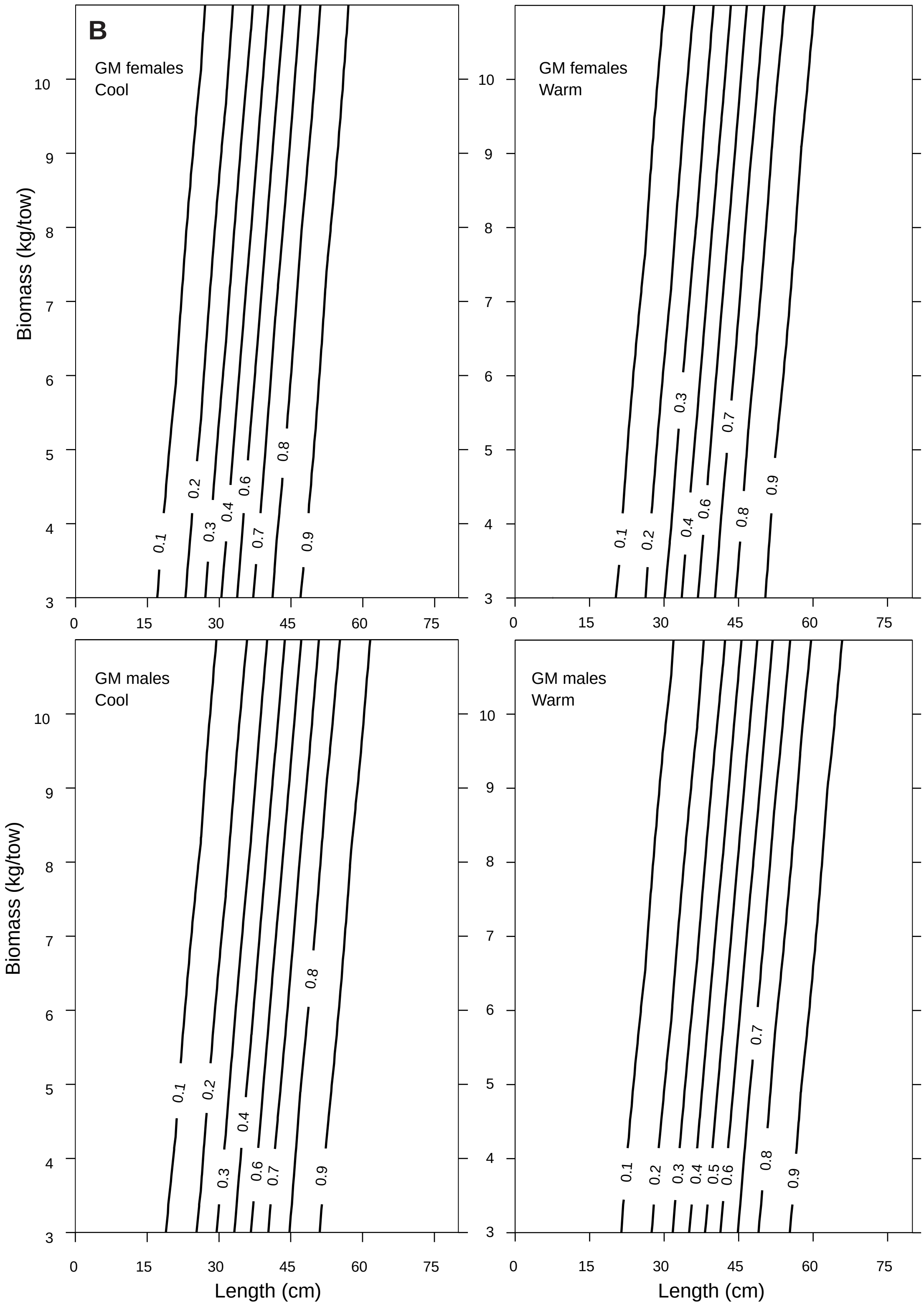

Fig. 4b. Simulated proportions mature at length for a range of biomasses at a cool and warm temperature for female and male Gulf of Maine (GM) Atlantic cod.

TABLE 4. Simulated proportions mature at length at both low (25th percentile) and high (75th percentile) bottom temperature anomaly (°C) and biomass (kg/tow) for a 45 cm and 33 cm Atlantic cod from Georges Bank and the Gulf of Maine, respectively, for females and males.

	Georges Bank (45 cm)				Gulf of Maine (33 cm)		
		Bottom Anomaly				Bottom Anomaly	
	Biomass	Low	High		Biomass	Low	High
Female	Low	67.0	68.0	Female	Low	45.1	41.5
	High	50.8	52.0		High	29.5	26.6
Male	Low	64.7	65.8	Male	Low	35.9	32.6
	High	48.3	49.5		High	22.2	19.8

TABLE 5. Parameter values and significance level of intercepts and slopes from analysis of covariance for difference in growth between sexes for Georges Bank and Gulf of Maine Atlantic cod 1970–76 year-classes (n = number of observations, ns is not significant, * is significant at $P = 0.05$, ** is significant at $P = 0.01$, – is intercept test invalid with significant slope).

Georges Bank								Gulf of Maine							
		Intercept			Slope					Intercept			Slope		
Year-class	n	Female		Male	Female		Male	Year-class	n	Female		Male	Female		Male
1970	390	–		–	40.20	**	33.48	1970	213	-2.30	*	-3.05	42.53	ns	41.02
1971	1646	–		–	42.49	**	38.81	1971	1057	–		–	47.51	*	43.97
1972	474	6.73	ns	6.18	44.50	ns	44.00	1972	121	-14.71	ns	-11.87	50.30	ns	46.24
1973	293	7.05	**	8.98	43.01	ns	39.19	1973	880	-10.98	*	-9.19	45.65	ns	43.28
1974	541	8.57	*	9.14	42.46	ns	40.59	1974	291	-10.42	ns	-5.99	47.78	ns	44.52
1975	1630	–		–	42.95	*	40.69	1975	323	-5.82	ns	-2.07	46.83	ns	42.90
1976	107	–		–	45.48	*	35.51	1976	113	-9.46	ns	-0.39	50.83	ns	46.47
1977	768	10.21	ns	11.95	41.44	ns	39.48	1977	437	-2.38	ns	-1.24	46.78	ns	45.81
1978	603	16.07	ns	7.30	36.86	ns	35.21	1978	282	7.83	ns	9.10	37.43	ns	35.60
1979	393	15.06	ns	14.17	37.20	ns	38.83	1979	197	2.87	ns	8.62	42.71	ns	38.84
1980	975	–		–	39.59	*	37.59	1980	311	7.68	ns	6.01	38.71	ns	39.66
1981	508	15.40	ns	15.78	38.80	ns	37.66	1981	228	8.51	ns	10.08	37.97	ns	36.50
1982	221	17.07	ns	14.90	35.48	ns	35.60	1982	208	4.52	ns	11.04	40.09	ns	35.80
1983	609	6.67	ns	7.53	43.34	ns	42.57	1983	250	1.34	ns	1.03	43.66	ns	44.46
1984	182	19.56	ns	13.12	33.82	ns	38.43	1984	207	0.41	*	0.75	41.49	ns	39.26
1985	923	–		–	36.48	**	33.36	1985	375	5.28	ns	5.95	37.55	ns	36.37
1986	302	11.18	ns	14.29	39.57	ns	36.46	1986	388	–		–	42.79	*	35.93
1987	592	12.35	ns	13.74	38.73	ns	36.72	1987	633	-2.28	*	-0.70	40.14	ns	37.64
1988	420	13.95	ns	16.31	37.41	ns	34.96	1988	84	–		–	47.21	*	33.61
1989	220	16.28	ns	15.95	34.17	ns	34.15	1989	77	-0.82	ns	6.62	39.29	ns	34.77
1990	489	–		–	38.22	**	33.14	1990	173	0.81	ns	4.58	42.07	ns	38.41
1991	231	11.56	ns	9.82	38.43	ns	38.96	1991	252	0.65	ns	5.30	38.57	ns	35.01
1992	369	0.85	ns	6.05	44.36	ns	39.83	1992	385	-1.57	ns	1.64	39.78	ns	36.39
1993	374	12.63	ns	13.67	37.57	ns	35.85	1993	111	13.81	ns	5.64	33.34	ns	38.59
1994	166	15.80	ns	7.94	36.28	ns	41.37	1994	121	14.05	ns	6.31	30.42	ns	34.95
1995	316	18.71	ns	14.77	30.58	ns	35.20	1995	55	15.84	ns	12.90	28.15	ns	30.22
1996	288	17.16	ns	18.47	31.78	ns	30.22	1996	73	13.16	ns	12.34	26.16	ns	28.04

The biological reference point, $F_{0.1}$, is dependent only upon the *PR* and declines by about 10% from the delayed *PR* to the early *PR* simulation. The fishing mortality at 20% of maximum spawning potential, $F_{20\%}$, is affected by both the *PR* and the maturation ogive. $F_{20\%}$ can increase or decrease

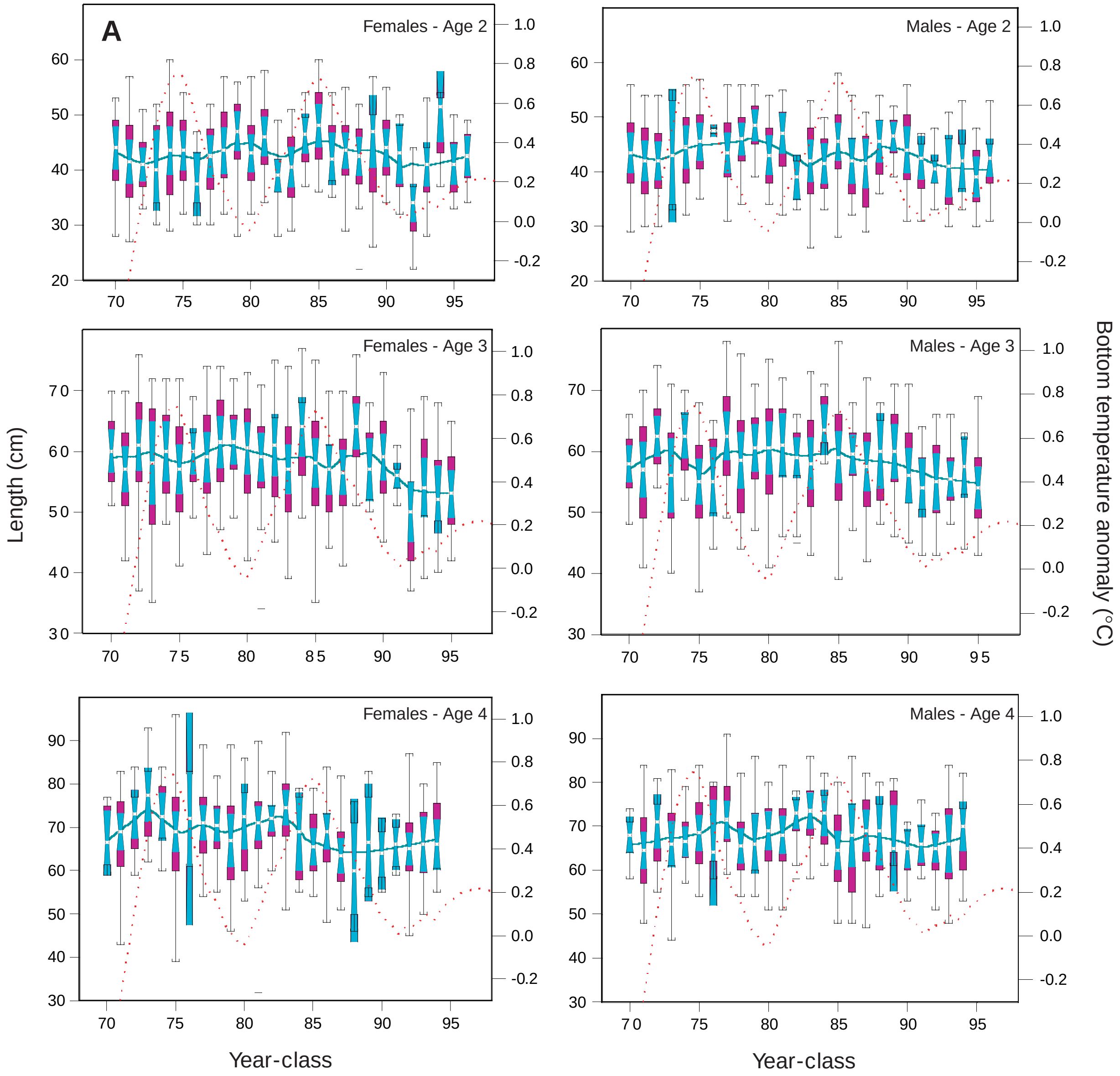

Fig. 5a. Box plot (white bar = median, blue bar = 95% confidence interval, red bar = 1st and 3rd quartiles overlaid with loess smooth (span = 0.2) of observed spring length-at-age data for ages 2–4 female and male Georges Bank Atlantic cod, by year-class. Dashed line is loess smooth (span = 0.3) of bottom temperature anomaly (°C).

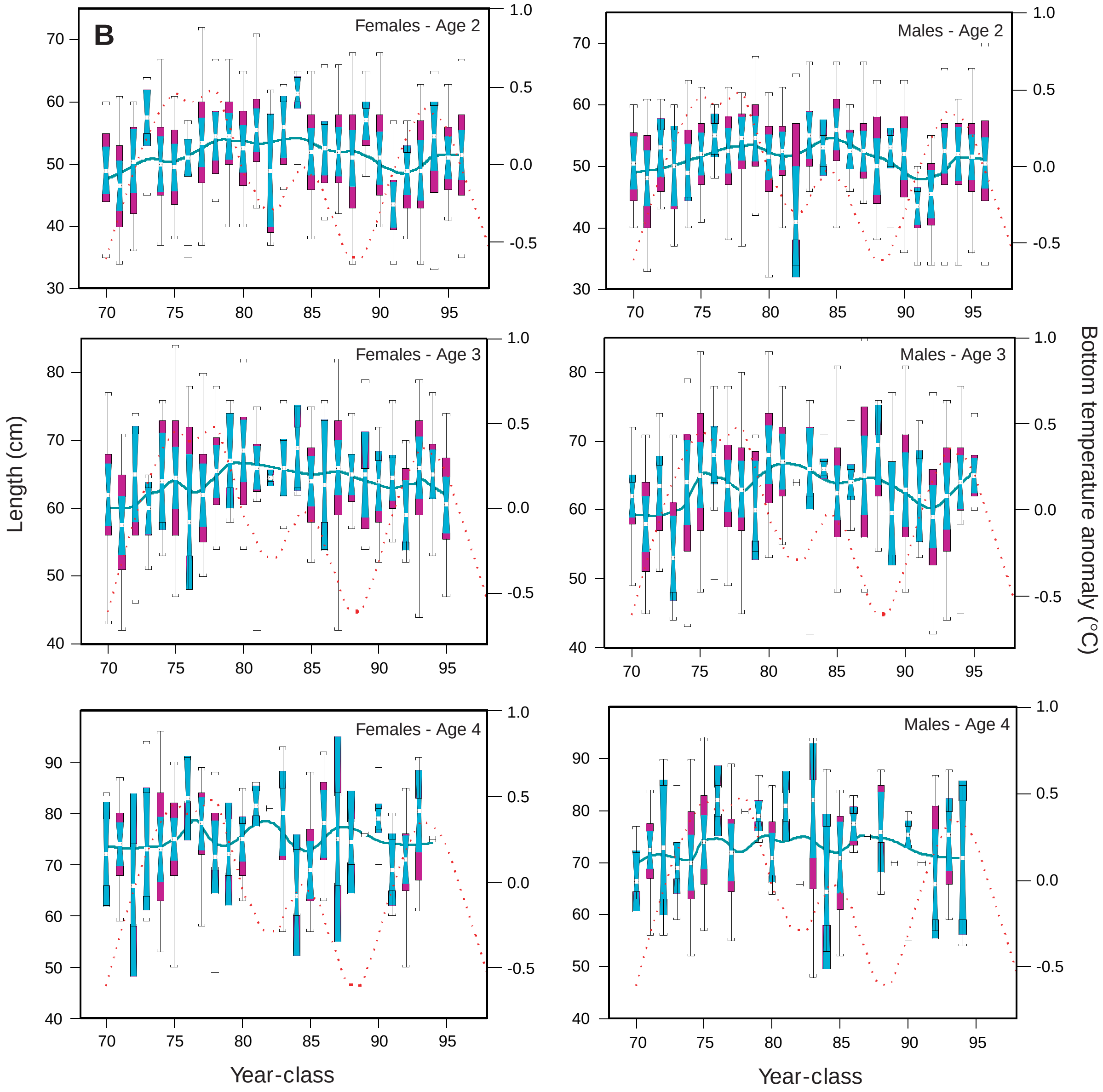

Fig. 5b. Box plot (white bar = median, blue bar = 95% confidence interval, red bar = 1st and 3rd quartiles overlaid with loess smooth (span = 0.2) of observed autumn length-at-age data for ages 2–4 female and male Georges Bank Atlantic cod, by year-class. Dashed line is loess smooth (span = 0.3) of bottom temperature anomaly (°C).

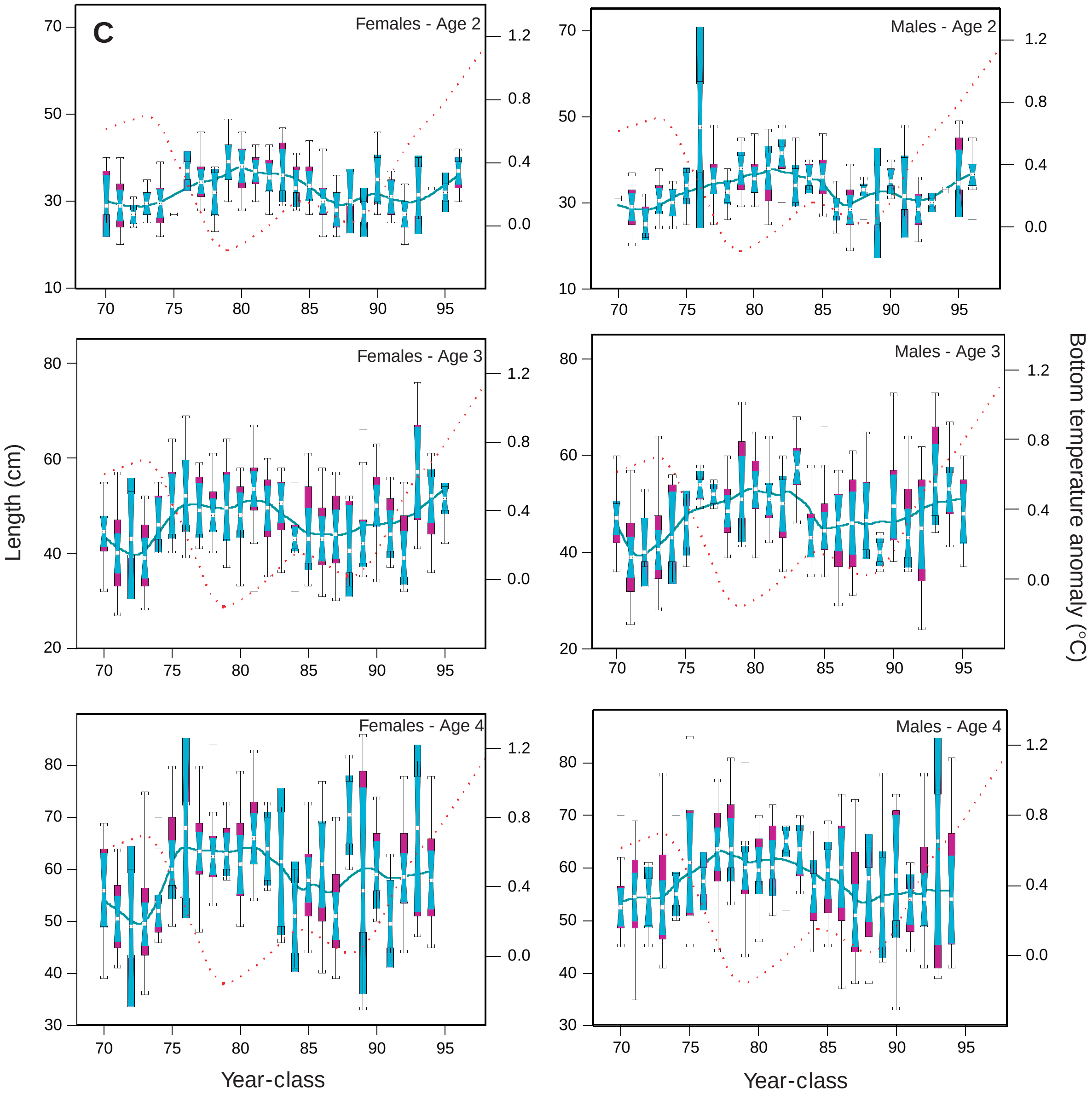

Fig. 5c. Box plot (white bar = median, blue bar = 95% confidence interval, red bar = 1st and 3rd quartiles overlaid with loess smooth (span = 0.2) of observed spring length-at-age data for ages 2–4 female and male Gulf of Maine Atlantic cod, by year-class. Dashed line is loess smooth (span = 0.3) of bottom temperature anomaly (°C).

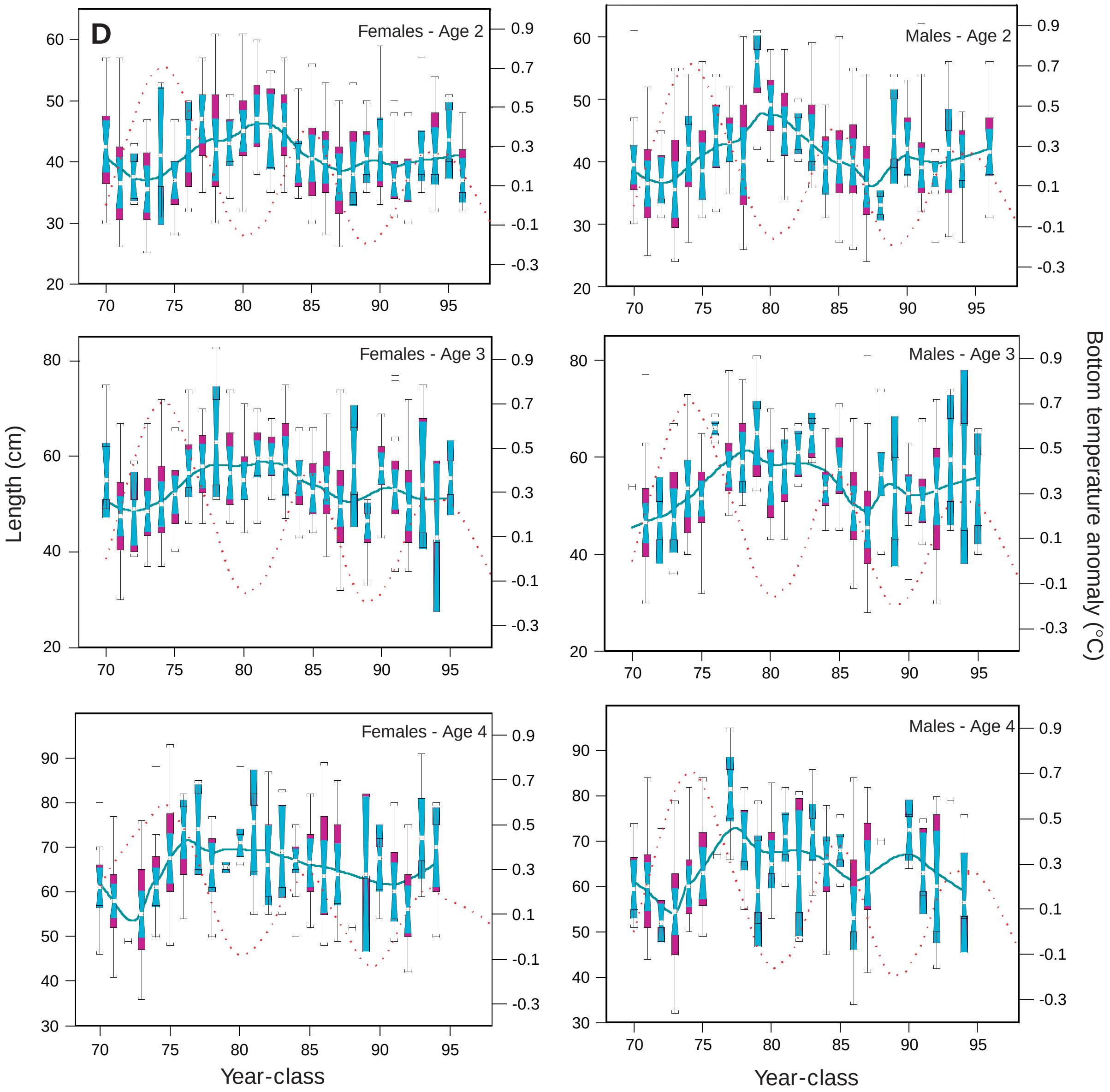

Fig. 5d. Box plot (white bar = median, blue bar = 95% confidence interval, red bar = 1st and 3rd quartiles overlaid with loess smooth (span = 0.2) of observed autumn length-at-age data for ages 2–4 female and male Gulf of Maine Atlantic cod, by year-class. Dashed line is loess smooth (span = 0.3) of bottom temperature anomaly (°C).

30% to 40% between the extremes of early maturation-delayed *PR* and late maturation-early *PR* (Fig. 7).

Discussion

There is subjectivity in the macroscopic classification of maturity stages of finfish, particularly, in differentiating between the immature and resting stage of the gonad (Halliday, 1987; Beacham, 1987; Hunter and Macewicz, 1985; Gunderson, 1977). However, analysis of gonado-somatic indices of Atlantic cod collected on NEFSC bottom trawl surveys indicated that macroscopic classification of maturity stages can be done reliably at sea (O'Brien, MS 1990). Although errors in classification of fish into mature stages may exist, i.e., developing *vs* ripe or spent *vs* resting, such mis-classifications would not affect L_{50} and A_{50} estimates. Measurement error can be reduced by collecting fish nearest the time of spawning

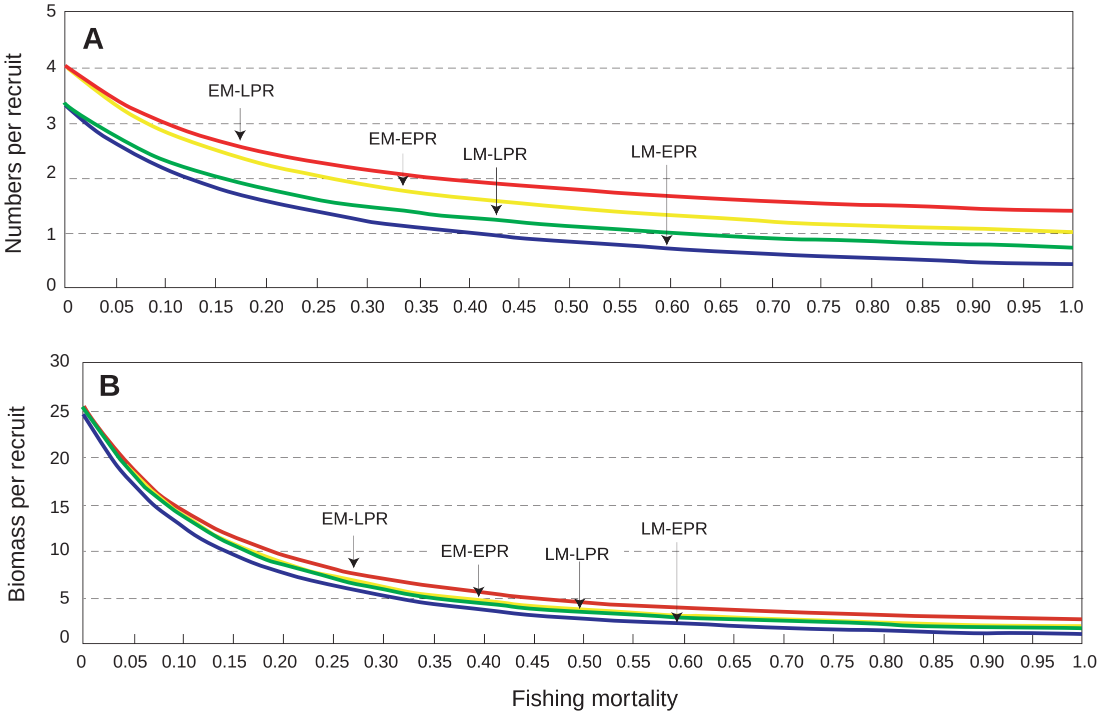

Fig. 6. Spawning stock numbers (panel A) and biomass (panel B) per recruit under four scenarios of 1) early maturation-early partial recruitment (EM-EPR), 2) early maturation-delayed partial recruitment (EM-DPR), 3) late maturation-early partial recruitment (LM-EPR), and 4) late maturation-delayed partial recruitment (LM-DPR) for fishing mortalities from 0 to 1.0.

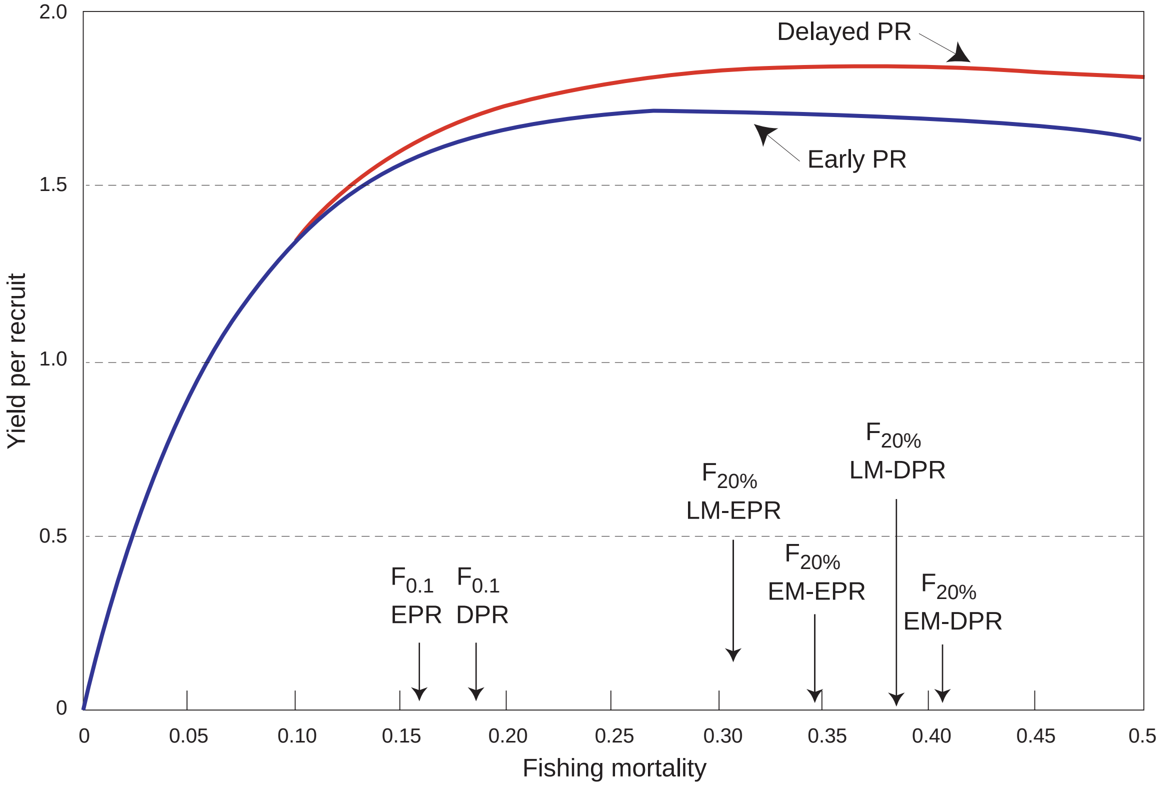

Fig. 7. Yield-per-recruit analysis for early (EPR) and delayed partial recruitment (DPR) with $F_{0.1}$ and $F_{20\%}$ at early (EM) and late maturation (LM).

(Halliday, 1987), when misidentifications between immature and resting fish are less likely to occur.

Estimates of L_{50} for the 1986–94 cohorts of Georges Bank cod derived in this study are generally less than for the same cohorts as estimated by Hunt (1996), and the 1986–95 annual estimates reported by Trippel *et al.* (1997). The differences may be attributed primarily to both the spatial and temporal collection of the maturity data. The NEFSC bottom trawl survey of Georges Bank, generally conducted in April, is about two months later than the February survey of Georges Bank conducted by the Canadian Department of Fisheries and Oceans (DFO). Although the DFO survey coverage is for all of Georges Bank (NAFO Div. 5Ze), the analysis of maturity data by Hunt (1996) and Trippel *et al.* (1997) was conducted for only the eastern part. The present analysis includes cod maturity data from all of NAFO Div. 5Ze. Other factors influencing the differences in estimates of median maturity may include slight differences in macroscopic identification of maturity stage and differences in treatment of the observations in the smallest and largest length groups which affects the tails of the logistic distribution.

The physical and environmental differences between Georges Bank and the Gulf of Maine are reflected in the different life history strategies for maturation and growth of Atlantic cod stocks from each area. The Georges Bank cod stock occupies a highly productive, shoal area, averaging 50 m with average bottom temperatures ranging from 4.0°C to 6.5°C in the spring and 8.6°C to 13.4°C in the autumn (Cohen and Grosslein, 1989; Uchupi and Austin, 1989; Holzwarth and Mountain, MS 1990). The Gulf of Maine stock occupies an area which has an average depth of 150 m, with a maximum depth of 377 m, and average bottom temperatures ranging from 5.1°C to 7.2°C in the spring and 5.8°C to 9.2°C in the autumn (Uchupi and Austin, 1989; Holzwarth and Mountain, MS 1990). Cod grow at different rates in the two areas during late spring, summer, and early autumn (Penttila, 1988). On Georges Bank, growth of cod is accelerated and maturation occurs about one year earlier compared to the cod in the Gulf of Maine. Differences in the age at maturation are expected when the growth rate differs between stocks of the same species (Alm, 1959). The warmer temperatures in the autumn and the high productivity of the Georges Bank area may contribute to the faster growth and earlier maturation of cod on Georges Bank compared to the slower growth and later maturation of cod from the Gulf of Maine. Differences in growth between the sexes within each stock are not as pronounced as differences between the stocks.

During the last three decades of intense exploitation neither cod stock has exhibited a persistent trend in growth. Although there have been shifts in the prey available to cod over this time period, it is unclear if the shifts have been substantial enough to warrant an increase or decrease in the growth rate of either stock (Jason Link, NEFSC, Food Web Dynamics Program; Woods Hole, MA, USA, pers. comm.). Daan (1974) also observed that the growth rate of North sea cod did not change during a period of increased fishing mortality.

The periods of increasing and decreasing growth, observed more in the Gulf of Maine than on Georges Bank, may be more related to temperature than to prey availability. The warming and cooling trends, while variable in both areas, appears to be more protracted in the Gulf of Maine than on Georges Bank. The influence of temperature on growth of cod has been noted for several cod stocks (Godø and Moksness, 1987; Brander, 1995). Further analyses of growth by size groups that include juvenile and maturing fish and incorporates weight at age and temperature effects would provide more definitive results.

Increased exploitation has contributed to decreased spawning stock biomass and a truncated age structure for both stocks and a decline in age and length at maturation. The results of this analysis suggest that the variation in maturation is influenced by both cod stock biomass and the environment, and that the timing of sexual maturity is determined during the juvenile phase. Chen and Mello (1999) also found that the age at which maturity was attained in NAFO Subdiv. 3Ps cod was influenced by the growth rate during the juvenile stage rather than at ages closer to maturity. In the North Sea plaice stock, the age at maturation was found to be mediated by growth rate or some associated factor during the early juvenile phase, prior to maturation about 3 years later (Rijnsdorp, 1993).

Variation in maturation without substantial changes in growth has been reported in other studies. Alm (1959) noted that maturity could vary among year-classes of the same stock even though growth and mean length remained constant from year to year. The variation was attributed to the temperature regime that fish were exposed to during the juvenile stage.

In a comparative study by Myers *et al.* (1997), age at maturity for 20 cod stocks was found to be significantly correlated with bottom temperature. During periods of increased exploitation median maturity declined in stocks of Cape horse mackerel, *Trachurus trachurus capensis* (Wysokinski, 1984) and North Sea cod (Oosthuizen and Daan, 1974) although the growth rate did not change in either stock. The northern stock of silver hake, *Merluccius bilinearis*, in the NAFO Subareas 5 and 6 exhibited declines in maturation with no change in growth; however, the southern stock in this region exhibited declines in both maturation and growth (Helser and Almeida, 1997).

The influence of both stock density and environment on age and length at maturity has also been noted for Baltic cod (Cardinale and Modin, 1999) and Northeast Arctic cod (Jorgensen, 1990) during periods of increased fishing mortality and declines in stock abundance. The size and age at maturity of Baltic cod were found to be significantly correlated with spawning stock biomass and the environmental factors, oxygen content and salinity level (Cardinale and Modin, 1999). Growth rate had not changed during the same time period (Larsson and Eriksson, 1995) although the hatch date of larvae had shifted, perhaps contributing to the decrease in size at maturity. In Northeast Arctic cod, a decline in age at maturity was related to increased growth as the stock declined, suggesting that growth may be density dependent for this stock (Jorgensen, 1990). Jakobsen (1992) further suggested the decline in age at maturity could be a response to long term changes in the environment despite no evidence of clear trends in temperature or ice conditions in the Barents Sea (Saetersdal and Loeng, 1987).

The analysis of variation in maturation predicted that temperature would influence proportion mature at length differently for the two stocks. The counter intuitive result of warmer temperature associated with lower proportions mature at length in Gulf of Maine cod is possibly an artifact of the model or may be related to energetics and the trade offs of growth and maturation (Roff, 1991). If warmer temperature increases productivity in general and provides more available resources, then the slower growing Gulf of Maine cod may divert surplus energy into somatic growth at the expense of gonadal growth (Jones and Johnston, 1974).

Smoothed survey biomass indices were applied in the analysis of variation in maturation instead of direct biomass estimates from VPA because the time series was too short. The contrast in the maturity data would have been lost if the time series was limited to available VPA biomass estimates. A disadvantage in using seasonal survey indices of biomass is the potential difference in catchability (*q*) of the surveys. On Georges Bank, the autumn survey index is consistently lower than the spring index which is reflected in the VPA estimate of a lower *q* for the autumn survey compared to the spring survey. The difference may be explained by the mortality imposed on the stock by the fishery between the two seasons. On Georges Bank, the Canadian fishery for cod begins in June, after the NEFSC spring survey, as did a portion of the USA fishery prior to 1994. This is in contrast to the Gulf of Maine, where the USA fishery is prosecuted primarily before the spring survey and where *q* is similar for both surveys.

Although assuming plasticity in the age at maturity violates the assumption of equilibrium in the yield-per-recruit analysis, the simulations illustrate the response of the stock to regime shifts in maturation on spawning stock per recruit and $F_{20\%}$, without changes in mean weight. In the long term, the best strategy for this stock would be maturation at a larger size and later age which was the likely condition of the stock when initially exploited. There are many advantages for delaying maturation, e.g. larger, heavier fish will be in better condition for spawning with higher fecundity and larger eggs that are more viable (Trippel and Morgan, 1994). Larger eggs will translate into larger larvae, which will have a competitive advantage for increased survival (Knutsen and Tielseth, 1985; Kjesbu *et al.*, 1996). Harvesting at a delayed *PR* enables the stock to maintain a high spawning biomass with an expanded age structure while supporting a sustainable fishery. If mortality on the stock increases and the *PR* shifts to earlier ages maturation will still be delayed at the larger sizes. This strategy is inherently risk-prone as the stock can be rapidly fished down. If the stock responds to continued exploitation by shifting maturity to an earlier age then spawning stock numbers will increase. The disadvantage of this strategy is that fish are spawning at smaller length and lower weight, such that the contribution to the spawning stock biomass is less than expected, given the large number of spawners. The other disadvantages are the opposite of spawning at a larger size: length and weight of the spawner is less, the fecundity is lower, eggs are smaller, and larvae are less viable (Solemdal, 1997) and smaller, which may be a competitive disadvantage for survival.

Selective mechanisms that form the reproductive strategy of a species are nearly impossible to detect in short term studies (Roff, 1983). Reduced adult survival will select for earlier maturation and increased reproductive effort (Gadgil and Bossert, 1970; Reznick, 1990). Earlier maturation is possibly a response of a stressed population in an environment that is more variable than when the stock is at a higher abundance (Garrod and Horwood, 1984; Rochet, 1998). The decline in maturation rate for both the Georges Bank and Gulf of Maine Atlantic cod stocks may be a response to increased adult mortality and declines in stock abundance.

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