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Factors Influencing Rates of Maturation in the Georges Bank and Gulf of Maine Atlantic Cod Stocks

by

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Stocks of Atlantic cod, *Gadus morhua*, off the coast of New England have been heavily exploited by domestic fisheries and abundance has declined in recent years. Maturation data collected by Northeast Fisheries Science Center research bottom trawl surveys from 1970-1997 were examined to determine if the rate of maturation of Atlantic cod exhibited compensatory responses to fluctuations in stock density and temperature. Median age and length at maturity by sex for the 1970-1994 year-classes was estimated using logistic regression.

Both age and length at maturity significantly declined during the past 25 years. To investigate potential causes for this decline, stepwise logistic regression was used to estimate the effect of stock density and temperature. Regressions were performed across all year-classes for each sex. Stock density explained a significant amount of the variation in maturation for both sexes from Georges Bank and the Gulf of Maine. Temperature explained a significant amount of the variation in the maturation for both sexes from Georges Bank but to a lesser extent for both sexes from the Gulf of Maine.

Introduction

Decreases in population density results in more resources being available for each individual in populations where density dependence is resource limited rather than regulated by predators (Gadgil and Bossert, 1970). A species may respond to less competition for resources by altering life history traits, including growth, longevity, sex ratio, fecundity, or age at maturity.

Compensatory responses of increased growth and accelerated maturation have been described for several exploited fish stocks that have experienced declines in population abundance (Stearns and Crandall, 1984;, Lett 1980; Ponomarenko, MS 1967; Beacham, 1982, 1983a, 1983b). De Veen (1976) found that as growth rates for North Sea sole *Solea solea* increased the length at maturity also increased. Density-dependent responses have been observed for haddock *Melanogrammus aeglefinus* (Templeman and Bishop, 1979) and Atlantic herring *Clupea harengus* (Sinclair *et al.*, MS 1980); when biomass declined in both species, the growth rates increased and length at maturity declined. Beacham (1983b) attributed the decline in length and age at maturation of the witch flounder *Glyptocephalus cynoglossus* to the fishery selectively removing the larger, later-maturing genotypes from the stock. Borisov (1978) simulated the effect of high annual fishing mortality on the reproductive contribution of different genotypes of the long-lived Arctic-Norwegian cod *Gadus morhua morhua*. The simulation indicated that the reproductive contribution of the late-maturing genotype would become negligible due to reduced abundance; however, the contribution of the early-maturing genotype would not be affected.

Selective removal of phenotypes by a fishery may lead to changes in the size or age of first maturation. When exploitation increased on a stock of Cape horse mackerel *Trachurus trachurus capensis*, Wysokinski (1984) observed declines in both the mean age of the population and median length at maturity but no alteration in the growth rate. A reduction in the length at maturity was considered to be a compensatory response since population levels remained high despite increasing fishing effort.

The above studies demonstrate that fish stocks are able to compensate for declines in biomass, induced through increased fishing pressure, by adapting growth or maturation, or both. Changes in growth and maturation, therefore, may be expected in Atlantic cod *Gadus morhua* stocks off the coast of New England, which have been heavily exploited in recent years by domestic fisheries.

Atlantic cod are distributed in the Northwest Atlantic from Port Burwell, West Greenland to Cape Lookout, North Carolina (Serchuk and Wood, MS 1979). Within the New England area, four distinct stocks are recognized (Wise, 1963): Georges Bank, Gulf of Maine, Southern New England and the South Channel, and the New Jersey coastal cod, which moves into the Southern New England stock area during the summer (Fig. 1).

These stocks are assessed for management purposes as the Gulf of Maine stock and the Georges Bank stock, which includes the Southern New England and South Channel, and the New Jersey coastal cod stocks. The Georges Bank cod stock occupies a highly productive (Cohen and Grosslein, 1989), shoal area, averaging 50 m (Uchupi and Austin, 1989) with average bottom temperatures ranging from 4.0-6.5 in the spring and 8.6-13.4 in the autumn (Holzwarth and Mountain, MS 1990). The Gulf of Maine stock occupy an area which has an average depth of 150 m, with a maximum depth of 377 m (Uchupi and Austin 1989), and average bottom temperatures ranging from 5.1-7.2 in the spring and 5.8-9.2 in the autumn (Holzwarth and Mountain, MS 1990). Atlantic cod are characterized as iteroparous spawners, i.e. successive breeding occurs more than once during the lifetime. The spawning season is from November to May: peak spawning on Georges Bank occurs during February and March and in the Gulf of Maine from March to May (Smith, 1985).

Abundance of Atlantic cod has decreased in recent years for both the Georges Bank and Gulf of Maine stocks, as indicated by low levels of both survey catch rate indices and estimates of stock size from virtual population analyses (Clark, 1998). Spawning stock biomass of Georges Bank cod declined from about 81 000 metric tons (mt) in 1978 to about 36 000 mt in 1997. Spawning stock biomass of Gulf of Maine cod declined from about 22 000 mt in 1982 to about 9 000 mt in 1997.

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). Age and length samples, and maturity observations for Atlantic cod have routinely been taken on each survey since 1970. In this analysis, data from 1970-1997 were partitioned by season into two areas, Georges Bank and the Gulf of Maine, corresponding to current Atlantic cod stock structure definition (NEFSC offshore bottom trawl strata 13-25, and strata 26-30 plus 36-40, respectively, Fig. 2).

At sea, length measurements were recorded to the nearest whole centimeter (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 otoliths by personnel at the NEFSC Woods Hole Laboratory according to procedures described by Penttila (1988).

Estimates of spring and autumn biomass of Atlantic cod were derived as stratified mean weight per tow (kg) and were obtained from the most recent assessment of the Georges Bank stock (O'Brien, MS 1998) and the Gulf of Maine stock (Mayo, MS 1998). Biomass time series were fit to an integrated moving average model to obtain smoothed indices (Fogarty *et al.*, MS 1986; Pennington, 1985, 1986). Smoothing the indices using this model filters the effects of measurement error in the survey data series from the 'true' variation in the population estimates (Fogarty *et al.*, MS 1986).

Spring and autumn biomass indices were lagged to associate each cohort with the cod biomass that cohort was exposed to during the juvenile developmental stage, up to age 2.5. For example, in the table below, the 1970 cohort was produced from the biomass of cod in the spring of 1970, and then developed as part of the 1970 autumn, 1971 spring, 1971 autumn, 1972 spring, and 1972 autumn biomass, up to age 2.5.

Smoothed Cod Abundance (kg/tow)

	Spring	Autumn	Cohort	lag 0	lag 0.5	lag 1.0	lag 1.5	lag 2.0	lag 2.5
1970	17.2	11.9	1970	17.2	11.9	18.3	13.0	21.0	15.2
1971	18.3	13.0							
1972	21.0	15.2							

Sea surface and bottom temperature anomalies were estimated from sea surface and bottom temperature samples taken during the spring and autumn NEFSC bottom trawl surveys for the 1970-1996 time series (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 temperature anomaly for both surface and bottom temperature was associated with each cohort up to age 2.5. The cumulative temperature anomaly is an indicator of whether a cohort has been exposed to warmer or colder waters during the juvenile life stage. For example, in the table below, the 1970 cohort was spawned in the spring of 1970 when the surface temperature anomaly was -0.6, by age 1 the cohort had been exposed to a cumulative anomaly of -1.8 (1970 spring +1970 autumn +1971 spring), and by age 2.5 the cumulative anomaly was -1.6.

Surface Temperature Anomaly

	Spring	Autumn	Cohort	lag 0	lag 0.5	lag 1.0	lag 1.5	lag 2.0	lag 2.5
1970	-0.6	-0.5	1970	-0.6	-1.1	-1.8	-0.8	-0.6	-1.6
1971	-0.7	1.0							
1972	0.2	1.0							

Maturity Analysis

The analysis was conducted using data from the spring bottom trawl survey for females and males by age and length from the 1970-1994 year-classes. Individual maturity observations were classified into either an immature or mature category. The mature category was classified by combining the developing, ripe, ripe and running, and resting stages.

The proportion of fish mature at length and age was estimated by fitting the logistic model (Ni and Sandeman, MS 1982; Gunderson, 1977; Haunschild *et al.*, MS 1983) to the proportion of mature fish calculated from sample data. The form of the logistic model used was:

$$P = 1 \;/\; (1 + e^{-(\alpha + \beta x)}) \qquad (1)$$

where: P = proportion mature,
x = either length or age,
α, β = model parameters to be estimated.

Parameter estimates of the model were obtained using logistic regression (SAS, 1990). Median maturity, defined as the length or age at which 50% of the fish are mature (L_{50} and A_{50} respectively), was calculated from the regression coefficients as [-(a/b)]. Linear regressions of L_{50} and A_{50} were conducted to test for significant trends in maturation over time. Any year-class value that did not have a significant fit to the model ($p < 0.05$) was excluded from the regression.

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.

Model Development / Stepwise Logistic (Logit) with Interactions

Stepwise logistic regression (SAS, 1990) with interaction terms was employed to develop models to determine if variation in maturation could be explained by factors of abundance and environment. The criteria for acceptance of the null hypothesis, that all independent variables are equal, was a significance level of 0.05. The logit form of the logistic was used for the analysis, where the logit can be expressed as

$$\operatorname{logit}(p) = \log \frac{p}{1-p} \qquad (2)$$

where p is equivalent to equation 1.

Equation (2) can be simplified and written in a linear form, with interaction terms:

$$\log \frac{p}{1-p} = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 \ldots \beta_n X_n \qquad (3)$$

Parameter estimates from the stepwise logistic regression can be substituted into equation 3 to derive the logit. Equation (1) can be rewritten as:

$$p = \frac{\exp(\beta_o + \beta_1 X_1 + \ldots)}{1 + \exp(\beta_o + \beta_1 X_1 + \ldots)} \qquad (4)$$

and the proportion mature can be estimated by substituting the logit into equation 4.

In the final series of models, the dependent variable was the observed proportion mature at age and length and the independent variables were length, lagged cod abundance, cumulative surface temperature anomaly, and the interaction terms of length x abundance and length x temperature anomaly. Two other model formulations were executed that were the same as described above, except that length was replaced as an independent variable with 1) age, and 2) age and length together. The analysis was done for each area, by sex, but not on a cohort basis as was done for the estimation of L_{50} and A_{50}. The Akaike Information Criterion or AIC (SAS, 1990) was used to determine the best fitting model where the lowest AIC indicates the best model. The AIC is a penalty function estimated using the log likelihood and the number of explanatory variables and ordered responses (SAS, 1990).

Growth analysis

A log-linear model (Bowers, 1960; Bowering and Brodie, 1984):

$$\text{length} = \alpha + (\beta \cdot \ln(\text{age})) \qquad (5)$$

was fitted to length-at-age data to predict mean length at age for females and males from Georges Bank and the Gulf of Maine. Length-at-age data for the 1970-1994 year-classes, 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.

Linear regressions of the predicted lengths at age were employed to detect significant trends in growth over the time series. The 1990-1994 year-classes were excluded so that the 1970-1989 year-class results were comparable with at least eight ages in each regression analysis.

To determine if mean lengths, adjusted for age, were similar between sexes, analysis of covariance (Sokal and Rohlf, 1981) was used to test the null hypotheses of equal slopes ( ) and equal y-intercepts ( ) between sexes for each year-class. The form of the model is:

$$Y_{ij} = \mu + \alpha_i + \beta_{within}(X_{ij} - \text{mean } X_{ij}) + \epsilon_{ij} \qquad (6)$$

where: Y_{ij} = length of jth observation for sex_i (i=1,2) or year-$class_i$ (i = 70,71...86),
μ = grand mean of the population,
α_i = fixed treatment effect for sex_i or year-$class_i$,
β_{within} = slope of the pooled regression within groups,
X_{ij} = ln(age); covariate,
$\beta_{within}(X_{ij}$ -mean X) = effect explained by the difference of the variate X_{ij} from the mean or X,
ϵ_{ij} = random deviation.

Simulation of Georges Bank Spawning Stock per Recruit under High and Low Exploitation

The effect of compensatory changes in maturation on the estimation of spawning stock per recruit for a cohort over its lifetime were simulated using an algorithm similar to that used for yield per recruit analyses (Thompson and Bell, 1934; Northeast Fisheries Center, 1984, Gabriel *et al.*, 1989). Spawning stock per recruit, in biomass and numbers, was estimated for fishing mortalities ranging from 0.1 to 1.0 under high and low exploitation patterns for the Georges Bank cod stock. The spawning stock per recruit (Gabriel *et al.*, 1989) in numbers (SSN) was calculated for each age (i = 1, 2, ...15) in a cohort as:

$$SSN_i = N_i \cdot PMAT_i \qquad (7)$$

where:
$N_i = N_{i-1} \cdot e^{-Z(i-1)}$,
$Z = (F \cdot PR_i) + M$,
F = fishing mortality,
PR_i = parital recruitment; fishing mortality at age i,
$PMAT_i$ = proportion of fish mature at age i.

The value of N for the youngest age is set equal to 1. The spawning stock per recruit in biomass (SSB) was calculated for each age in a cohort as:

$$SSB_i = SSN_i \cdot MWT_i , \qquad (8)$$

where MWT_i = mean weight at age i. Total spawning stock per recruit (in numbers and biomass) for a cohort was obtained by summing SSN_i and SSB_i over all ages. The natural mortality was estimated as M = 0.2 (Serchuk and Wigley, MS 1986). Mean weights at age were kept constant using the current population weights from the most recent Georges Bank cod assessment (O'Brien, MS 1998). Partial recruitment at age was calculated by dividing age specific fishing mortality (O'Brien, MS 1998) by the mean F for fully recruited age 4-8 fish. Partial recruitment estimates represent the proportion of fully recruited F that is applied to ages 1-3 fish. Garrod (1988) defines these proportions as an exploitation pattern. Fishing mortality estimates for years of low (1979) and high exploitation (1985) patterns were obtained from virtual population analysis (O'Brien, MS 1998) encompassing the period 1978-1997.

Spawning stock per recruit analyses (in biomass and numbers) were performed for two cases which represent actual stock conditions prior to and after increased exploitation: 1) low exploitation rate in 1979 with late maturation (A_{50} is at an older age), and 2) high exploitation rate in 1985 with early maturation (A_{50} is at a younger age). A third scenario simulated a high exploitation rate and late maturation to evaluate the spawning stock per recruit in the absence of a change in maturation but with increased exploitation. Annual maturation schedules were derived from the proportion of mature Georges Bank females predicted by the logistic model for year-classes. The late maturation schedule (1977) consisted of the percentage of mature 1 year old females from the 1976 year-class, the percentage of mature 2 year old females from the 1975 year-class, etc. Similarly, the early maturation schedule (1985) consisted of mature 1 year old fish from the 1984 year-class, mature 2 year old fish from the 1983 year-class, etc.

Results

Maturity Analysis

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. The following year-classes did not have a significant fit to the model: Georges Bank males - 1976 for age, and 1982, 1992, and 1994 for length; Gulf of Maine females -1976, 1988, and 1994 for age, and 1988 and 1994 for length; Gulf of Maine males - 1984, 1988, 1993, and 1994 for age and 1988 for length (Table 1).

Georges Bank and Gulf of Maine year-classes of cod had L_{50} and A_{50} values that ranged from 30 to 58 cm and from 0.8 to 4.3 years, respectively (Table 1). For Georges Bank year-classes, L_{50} for females varied between 31 cm (1985) and 57 cm (1972) and L_{50} for males varied between 37 cm (1984) and 56 cm (1972). A_{50} for females varied between 0.8 years (1985) and 2.9 years (1972-1973) and for males A_{50} values varied between 1.4 years (1989) and 3.1 years (1973) (Table 1, Fig. 3).

Year-class values of L_{50} for Gulf of Maine females varied between 30 cm (1987) and 58 cm (1970) and L_{50} for males varied between 28 cm (1983) and 54 cm (1970). A_{50} values for females varied between 1.4 years (1975) and 4.3 years (1970) and for males, A_{50} values varied between 1.1 years (1983) and 4.3 years (1970) (Table 1, Fig. 4).

The age at 100% maturity, although variable, has generally declined by one age throughout the time series for both areas (Table 2). The earlier Georges Bank year-classes attained 100% maturity between ages 5 and 6, with a decrease to ages 4 and 5 in the later year-classes for both sexes. The earlier Gulf of Maine year-classes attained 100% maturity between ages 6 and 7, with a decrease to ages 5 and 6 in the later 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 for all cases for both Georges Bank and the Gulf of Maine females and males. Data are presented in Fig. 3 and 4, and are fitted to a loess smooth. The difference in the average maturation for the first 5 (1970-1974) and last (1990-1994) 5 year-classes indicate a decline in L_{50} of about 9-14 cm and 11 cm for Georges Bank and Gulf of Maine year-classes, respectively. A_{50} also declined about 0.6-0.8 years and 1.2-1.4 years for Georges Bank and Gulf of Maine year-classes, respectively.

Linear regression analysis of the percentage mature at age against the time series showed significant differences from a slope of zero ($P < 0.05$) for age 2 and age 3. The percentage mature at age 2 significantly increased over the time series for both sexes on Georges Bank (Fig. 5) but the slope was not significantly different from zero for either sex in the Gulf of Maine. The percentage mature at age 3 significantly increased over the time series for both Georges Bank and Gulf of Maine females and males (Fig. 6).

Model Development / Stepwise Logistic (Logit) with Interactions

Stepwise logistic models with age as an independent variable gave consistently higher AIC values than the models with length as an independent variable. Models with both length and age as independent variables had AICs that were either equal to or slightly less the AIC for models with length only. Since the age variable did not consistently lower the AIC, the final models were chosen using length as an independent variable.

The final models that best explains variation in maturation are described by all or a combination of the independent variables of length (Len), cod biomass (Den), surface temperature anomaly, (Temp), and the interaction terms of length x density and length x temperature for each stock, by sex (Table 3). All variables, within an area and sex, were lagged on the same time scale.

Georges Bank females: variables at a 2.5 year lag :

$$\text{logit} = -5.9275 + 0.1598*\text{Len} - 0.1656*\text{Den} + 0.0022*\text{Len}*\text{Temp}$$

Georges Bank males: variables at a 2.5 year lag logit = -6.3968 + 0.1613*Len - 0.137 *Den + 0.1011*Temp

Gulf of Maine females: variables at a 0 year lag.

logit = -1.728 + 0.1046*Len - 0.6046*Den + 0.0061*Len*Den + 0.0056*Len* Temp

Gulf of Maine males: variables at a 2.5 year lag.

logit = -2.167 + 0.081*Len - 0.484*Den + 0.0067*Len*Den + 0.0019*Len*Temp

Results of models indicate that the biomass of cod and surface temperature influence the rate of maturation of cod. For example, at constant biomass, for a 45 cm Georges Bank female cod, comparison of percent mature at length between high and low temperature anomaly indicates that at a low anomaly (cooler temperature) the proportion mature is 51% compared to 67% at a high anomaly (warmer temperature). This implies that at warmer temperatures, 17% more of the 45 cm females would mature than at lower temperatures, at a constant cod biomass (Fig. 7a, 7b, 8a, and 8b).

Growth analysis

The predicted mean length at age of female and male cod appears to have generally increased for younger ages and decreased for older ages both on Georges Bank and in the Gulf of Maine (Fig. 9a-d). Among the 1970-1994 year-classes, predicted mean lengths-at-age of females and males varied between 8-22 cm for Georges Bank (Table 4a and 4b, Fig. 9a and 9b) and between 14-55 cm for Gulf of Maine cod (Table 5a and 5b, Fig. 9c and 9d). The greatest variation in predicted mean lengths occurred in the older ages, and the smallest variation occurred in ages 2 and 3 in both stocks.

Linear regressions of predicted mean lengths for year-classes 1970-1989, indicated a significant departure from a slope of zero primarily for Georges Bank females. On Georges Bank, age 1 and 2 females and age 1 males exhibited a significant increase in growth over time (Table 6). A similar pattern for younger ages was seen in the Gulf of Maine, where the length of age 1 fish significantly increased over time for both females and males. The growth of age 4-8 fish significantly decreased over time for Georges Bank females but not for males. There were no significant declines in growth of the older age classes in the Gulf of Maine (Table 6). Although the results were not significant, the mean length of mature males from Georges Bank, and mature females and males from the Gulf of Maine also appear to show a generally declined since 1977.

Analysis of covariance indicated, for both Georges Bank and Gulf of Maine cod, that females grew faster (i.e. had higher slopes) than males in most year-classes, however, the more recent years classes of males in the Gulf of Maine grew faster than females (Table 7).

On Georges Bank, females generally grew at a faster rate than males, but this difference was only significant in 11 of the 27 year-classes. The null hypothesis of equal slopes between the sexes was rejected ($P < 0.05$) for 1970, 1971, 1975, 1976, 1980, 1985, 1990, 1992, and 1994 year-classes (Table 7). The slopes of the 1973 and 1974 year-class regression equations were statistically similar for the two sexes, but the y-intercept values were significantly different ($P < 0.05$).

In the Gulf of Maine, females generally grew at a faster rate than males, however, this difference was only significant in 7 of the 27 year-classes (Table 7). The null hypothesis of equal slopes between the sexes was rejected for the 1971, 1986, 1988, 1994 year-classes. The y-intercepts of the 1970, 1971, 1973, and 1987 year-class regression equations were statistically different ($P < 0.05$) for the two sexes.

Spawning Stock per Recruit Analysis

The spawning stock per recruit model showed that with increased exploitation the compensatory response of earlier maturation increases the spawning number per recruit but decreases the spawning biomass per recruit (Fig. 10a and 10b). The simulation of stock conditions prior to increased exploitation, represented by a late maturation-low exploitation pattern, showed that spawning numbers per recruit would decline from 3.4 at $F = 0.0$ to 0.65 at F

= 1.00 (Fig. 10a). Spawning biomass per recruit would decline from 25 kg at F = 0.0 to 1.5 kg per recruit at F = 1.00 at low exploitation (Fig. 10b).

For the simulation of early maturation-high exploitation, spawning numbers per recruit would be greater than the late maturation-low exploitation scenario, declining from 3.9 at F = 0.0 to 0.87 fish per recruit at F = 1.00 (Fig. 10a). The spawning biomass per recruit would be slightly less than the late maturation-low exploitation scenario for all values of F (Fig. 10b). The simulated stock conditions of late maturation-high exploitation showed that spawning number per recruit would initially be equal to the late maturation-low exploitation condition, but would decrease more rapidly with increasing F to 0.43 fish per recruit at F = 1.00 (Fig. 10a). Spawning biomass per recruit would initially be similar to the early maturation-high exploitation conditions (25 kg at F = 0.0, 0.9 kg at F = 1.00) but still less than the values of either the late maturation-low exploitation or the early maturation-high exploitation simulation (Fig. 10b).

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 gonadosomatic 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, 1990). Although errors in classification of fish into mature stages may exist, i.e. developing *vs.* ripe or spent *vs.* resting, such misclassifications would not affect L_{50} and A_{50} estimates. Measurement error can be reduced by collecting fish nearest the time of spawning (Halliday, 1987), when misidentifications between immature and resting fish are less likely to occur. Peak spawning for Atlantic cod occurs in the spring on Georges Bank (February-March) and in the Gulf of Maine (March-May) areas (Smith, 1985), so the spring maturity data were analyzed for the estimation of maturation.

The physical and environmental differences between Georges Bank and the Gulf of Maine are reflected in the life history strategies of the two cod stocks. The rates of maturation and growth differ in the two areas; maturation occurs at an earlier age for cod on Georges Bank and growth is accelerated compared to the Gulf of Maine cod. Difference in the age at maturation would be expected given the different growth rates of the two stocks (Penttila, 1988). The difference in maturation rate between the two areas is more evident from the percent mature at age 2 and 3 than from actual A_{50} values. The plasticity in maturation is in age 2 and age 3 year old fish on Georges Bank, and but only in the 3 year old fish in the Gulf of Maine. This is in agreement with the slower growth of Gulf of Maine cod, reflected in the smaller mean lengths-at-age.

Cod grow during the late spring, summer, and early fall (Penttila, 1988). The warmer temperatures in the autumn and the higher productivity of the Georges Bank area may contribute to the faster growth and earlier maturation of cod on Georges Bank compared to cod from the Gulf of Maine. Differences in growth between the sexes within each stock are not as pronounced as differences between the stocks.

Increased exploitation has contributed to a decrease in the spawning stock biomass of both stocks through the selective removal of the faster growing, larger and later maturing fish, during the last two decades. This is most evident from the decline in mean length of Georges Bank females. Both stocks have compensated similarly for their truncated age structure by increasing the rate of growth of young fish and with simultaneous adjustments to the age and length at maturation so that fish mature at an earlier age and smaller size. Averaging female and male responses, the Gulf of Maine stock exhibited a decrease in age at maturation of about 0.5 year more than the Georges Bank stock, whereas the change in length at maturation was similar at about 11 cm on average for both areas. Georges Bank cod, being in a more productive area may be growing at their maximum rate under the optimum conditions of temperature and food availability and may have reached a physiological limit for decreasing age at maturity. Gulf of Maine cod, however, are in a less optimal area, and may display more plasticity in age at maturation channeling excess energy into gonadal growth, resulting in earlier maturation. In a similar study, Daan (1974) reported that the growth rate of North Sea cod did not change during a period of increased fishing mortality although age at maturation declined (Oosthuizen and Daan, 1974).

That cod exhibit age-dependent maturation, with more variability in length at maturation, is evidenced by the logit models, where length was more influential than age as an independent variable. A compilation of median age and length at maturity data for 18 gadiforms and pleuronectiforms in the Georges Bank and Gulf of Maine region of the Northwest Atlantic indicated that the gadids generally exhibited age-dependent maturation i.e. maturation occurs by a certain age over a range of lengths, compared to flounders, which exhibited length-dependent maturation, i.e. maturation occurs by a certain length over a range of ages (O'Brien *et al.*, 1993).

The effect of accelerated rate of maturation on stock dynamics is not easily quantified given all the variables that are likely involved and difficult to measure, but the impact can perhaps be seen in the strength of subsequent year-classes. When a year-class matures at an early age in response to declining biomass, the maximum stock fecundity may be adversely affected due to decreased egg viability and reduced individual fecundity of younger fish, and increased mortality due to the stress of spawning. Fecundity, defined as the number of eggs in the ovaries of female fish, increases with size and attains a maximum at the asymptotic body weight (Moyle and Cech, 1982). Currently, on Georges Bank, where A_{50} for cod occurs at age 2, with 100% maturation at ages 5-6, and full recruitment to the gear occurring by age 3, the maximum stock fecundity is not being realized as the cohorts decline at a relatively rapid rate. Since 1970 there have been several relatively strong year-classes, but each has been weaker than the previous relatively strong year-class (O'Brien, MS 1998; Mayo, MS 1998). The probability of a obtaining a strong year-class is less when the stock is dominated by first time spawners compared with a spawning stock comprised of many mature year-classes. Ponomarenko (1973) suggests two hypotheses for the probability of stronger year-classes occurring with a higher abundance of repeat spawners: 1) repeat spawners lay eggs of higher quality, thus larvae and fingerlings are more viable and 2) with more spawning ages in the spawning biomass the duration of spawning is increased as well as the spawning area. An implicit assumption in the second hypothesis is that different age groups begin spawning at different times within the spawning season.

The maturation rate of Georges Bank cod is influenced by both biomass and temperature, whereas maturation of Gulf of Maine cod is mostly influenced by biomass. The lesser influence of temperature on maturation rate in the Gulf of Maine may be due to less variability in surface temperatures. Sea surface temperature anomalies vary within only 2 degrees in both spring and autumn in the Gulf of Maine but on Georges Bank, the temperature anomalies vary more in the autumn, by about 4 degrees.

Assuming plasticity in the age and length at maturity (Stearns and Crandall, 1984), the spawning stock per recruit model demonstrated how compensatory responses in maturation to increased exploitation affects the estimation of spawning numbers and biomass per recruit.

Not surprisingly, the best strategy for this stock, to attain high spawning stock biomass per recruit, would be late maturation under low exploitation rates, 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. Larger eggs will translate into larger larvae, which will have a competitive advantage for increased survival.

The strategy of late maturation under conditions of high exploitation is inherently risk-prone as the stock would be fished down rapidly leading to collapse. Alternatively, the stock can mature early under high exploitation resulting in larger numbers of mature fish per recruit. 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 less viable, and the smaller larvae will be at a competitive disadvantage.

Selective mechanisms that form the reproductive strategy of a species are nearly impossible to detect in short term studies (Roff, 1983). Although the mechanism of compensation is undetermined, the evidence that Atlantic cod compensate for fluctuations in stock abundance is clear. Both Georges Bank and Gulf of Maine cod have responded to stress imposed on the stock by altering age and length at maturation, and increasing growth of immature fish. These changes in life history strategy are not without cost. Potential trade-offs for maturing earlier include decreased egg viability, lower fecundity, and increased mortality. Without sufficient number of older age groups comprising the spawning stock biomass the reproductive output of the stock is potentially reduced. These results imply that in order to maintain a sustainable fishery on these stocks, the spawning stock biomass needs to be comprised of an expanded age structure of late maturing fish to buffer the stock against environmental perturbations and high exploitation.

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TABLE 1. Age and length at 50% maturation for female and male Atlantic cod from Georges Bank and Gulf of Maine for year-classes 1970-1994 estimated from spring data (ns = not significant).

Year-class	Age Georges Bank Spring females	 males	 Gulf of Maine Spring females	 males	Length Georges Bank Spring females	 males	 Gulf of Maine Spring females	 males
70	2.70	2.29	4.30	4.26	53.71	47.98	58.30	54.40
71	2.84	2.84	3.85	3.87	53.96	52.34	49.93	49.89
72	2.88	2.79	3.07	3.72	57.22	56.29	43.01	48.47
73	2.88	3.05	3.87	4.04	53.98	53.42	47.82	50.89
74	2.66	2.46	3.12	3.55	55.45	52.20	44.71	50.36
75	2.24	2.32	1.36	2.96	46.92	47.78	34.10	42.71
76	2.15	ns	ns	2.96	42.50	45.71	38.52	53.27
77	2.31	2.69	2.51	3.30	47.55	54.04	42.00	53.77
78	2.40	2.80	2.22	2.74	50.05	54.19	35.23	45.05
79	2.42	2.61	2.32	2.50	50.93	54.25	43.08	43.99
80	2.11	2.23	2.49	2.56	44.35	46.54	42.73	44.63
81	1.97	1.78	2.41	2.39	44.02	41.90	42.30	43.62
82	2.58	2.80	2.20	2.05	49.99	ns	40.69	39.57
83	2.01	1.81	1.92	1.07	40.69	40.05	30.29	27.89
84	1.74	1.95	1.83	ns	42.09	36.55	34.38	32.53
85	0.82	1.71	1.96	2.22	31.29	40.41	33.30	36.96
86	2.02	2.15	2.20	2.54	40.43	43.40	31.84	36.19
87	2.67	2.03	2.21	3.66	41.85	41.84	30.05	48.28
88	1.90	1.73	ns	ns	34.72	39.37	ns	ns
89	1.65	1.38	3.15	3.77	41.72	39.13	43.37	48.39
90	2.15	2.36	2.76	3.00	46.84	47.89	44.91	47.10
91	1.68	2.13	2.23	1.88	36.01	43.23	33.74	34.73
92	2.53	2.09	2.55	2.54	42.26	na	33.20	33.79
93	1.91	1.89	2.06	ns	38.33	39.54	36.09	33.22
94	1.83	2.00	ns	ns	43.09	ns	ns	48.75
min	0.82	1.38	1.36	1.07	31.29	36.55	30.05	27.89
max	2.88	3.05	4.30	4.26	57.22	56.29	58.30	54.40

Table 2. The percentage of female and male Atlantic cod mature-at-age for the 1970-1994 year-classes for Georges Bank and the Gulf of Maine based on data collected on spring research surveys.

	Georges Bank Females								Georges Bank Males								Gulf of Maine Females								Gulf of Maine Males							
	Age								Age								Age								Age							
Year-class	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
70	0.02	0.17	0.66	0.95	0.99	1.00	1.00	1.00	0.12	0.39	0.75	0.93	0.99	1.00	1.00	1.00	0.00	0.02	0.10	0.38	0.76	0.95	0.99	1.00	0.02	0.07	0.19	0.43	0.70	0.88	0.96	0.99
71	0.01	0.09	0.61	0.96	1.00	1.00	1.00	1.00	0.01	0.13	0.59	0.94	0.99	1.00	1.00	1.00	0.00	0.01	0.12	0.58	0.93	0.99	1.00	1.00	0.00	0.03	0.16	0.56	0.90	0.98	1.00	1.00
72	0.02	0.14	0.56	0.91	0.99	1.00	1.00	1.00	0.01	0.12	0.63	0.96	1.00	1.00	1.00	1.00	0.00	0.00	0.33	1.00	1.00	1.00	1.00	1.00	0.03	0.11	0.29	0.58	0.83	0.94	0.98	0.99
73	0.05	0.20	0.55	0.85	0.97	0.99	1.00	1.00	0.02	0.13	0.48	0.85	0.97	1.00	1.00	1.00	0.01	0.05	0.20	0.55	0.86	0.97	0.99	1.00	0.01	0.04	0.17	0.48	0.81	0.95	0.99	1.00
74	0.00	0.10	0.76	0.99	1.00	1.00	1.00	1.00	0.05	0.29	0.74	0.95	0.99	1.00	1.00	1.00	0.00	0.04	0.41	0.93	1.00	1.00	1.00	1.00	0.01	0.05	0.25	0.71	0.95	0.99	1.00	1.00
75	0.06	0.36	0.85	0.98	1.00	1.00	1.00	1.00	0.06	0.34	0.80	0.97	1.00	1.00	1.00	1.00	0.43	0.63	0.79	0.90	0.95	0.98	0.99	1.00	0.00	0.00	0.60	1.00	1.00	1.00	1.00	1.00
76	0.08	0.42	0.85	0.98	1.00	1.00	1.00	1.00	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.00	0.00	0.60	1.00	1.00	1.00	1.00	1.00
77	0.19	0.42	0.68	0.87	0.95	0.98	0.99	1.00	0.17	0.34	0.57	0.78	0.90	0.96	0.98	0.99	0.08	0.30	0.69	0.92	0.98	1.00	1.00	1.00	0.03	0.12	0.39	0.74	0.93	0.98	1.00	1.00
78	0.06	0.31	0.76	0.96	0.99	1.00	1.00	1.00	0.02	0.14	0.62	0.94	0.99	1.00	1.00	1.00	0.05	0.37	0.87	0.99	1.00	1.00	1.00	1.00	0.07	0.25	0.59	0.86	0.96	0.99	1.00	1.00
79	0.03	0.27	0.80	0.98	1.00	1.00	1.00	1.00	0.01	0.14	0.76	0.98	1.00	1.00	1.00	1.00	0.17	0.40	0.69	0.88	0.96	0.99	1.00	1.00	0.12	0.34	0.66	0.88	0.96	0.99	1.00	1.00
80	0.07	0.44	0.89	0.99	1.00	1.00	1.00	1.00	0.03	0.34	0.91	0.99	1.00	1.00	1.00	1.00	0.07	0.30	0.71	0.93	0.99	1.00	1.00	1.00	0.01	0.15	0.80	0.99	1.00	1.00	1.00	1.00
81	0.07	0.52	0.94	1.00	1.00	1.00	1.00	1.00	0.18	0.60	0.91	0.99	1.00	1.00	1.00	1.00	0.00	0.17	0.91	1.00	1.00	1.00	1.00	1.00	0.00	0.16	0.93	1.00	1.00	1.00	1.00	1.00
82	0.04	0.23	0.70	0.95	0.99	1.00	1.00	1.00	0.00	0.00	0.94	1.00	1.00	1.00	1.00	1.00	0.00	0.05	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.38	1.00	1.00	1.00	1.00	1.00	1.00
83	0.03	0.49	0.97	1.00	1.00	1.00	1.00	1.00	0.16	0.60	0.92	0.99	1.00	1.00	1.00	1.00	0.00	0.70	1.00	1.00	1.00	1.00	1.00	1.00	0.47	0.78	0.93	0.98	1.00	1.00	1.00	1.00
84	0.20	0.62	0.92	0.99	1.00	1.00	1.00	1.00	0.00	0.63	1.00	1.00	1.00	1.00	1.00	1.00	0.20	0.57	0.88	0.97	1.00	1.00	1.00	1.00	--	--	--	--	--	--	--	--
85	0.54	0.76	0.90	0.96	0.98	0.99	1.00	1.00	0.27	0.60	0.85	0.96	0.99	1.00	1.00	1.00	0.19	0.51	0.83	0.95	0.99	1.00	1.00	1.00	0.06	0.38	0.86	0.98	1.00	1.00	1.00	1.00
86	0.13	0.49	0.86	0.98	1.00	1.00	1.00	1.00	0.09	0.42	0.85	0.98	1.00	1.00	1.00	1.00	0.02	0.35	0.93	1.00	1.00	1.00	1.00	1.00	0.11	0.32	0.65	0.88	0.97	0.99	1.00	1.00
87	0.13	0.32	0.59	0.82	0.94	0.98	0.99	1.00	0.19	0.49	0.80	0.94	0.98	1.00	1.00	1.00	0.29	0.46	0.64	0.79	0.89	0.94	0.97	0.99	0.15	0.26	0.40	0.55	0.70	0.82	0.89	0.94
88	0.00	0.79	1.00	1.00	1.00	1.00	1.00	1.00	0.20	0.62	0.91	0.99	1.00	1.00	1.00	1.00	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
89	0.29	0.62	0.87	0.96	0.99	1.00	1.00	1.00	0.40	0.66	0.85	0.95	0.98	0.99	1.00	1.00	0.01	0.06	0.41	0.89	0.99	1.00	1.00	1.00	0.01	0.04	0.20	0.60	0.90	0.98	1.00	1.00
90	0.01	0.34	0.98	1.00	1.00	1.00	1.00	1.00	0.01	0.23	0.90	1.00	1.00	1.00	1.00	1.00	0.00	0.08	0.69	0.98	1.00	1.00	1.00	1.00	0.00	0.00	0.50	1.00	1.00	1.00	1.00	1.00
91	0.09	0.74	0.99	1.00	1.00	1.00	1.00	1.00	0.09	0.44	0.86	0.98	1.00	1.00	1.00	1.00	0.01	0.31	0.94	1.00	1.00	1.00	1.00	1.00	0.24	0.54	0.82	0.94	0.98	1.00	1.00	1.00
92	0.00	0.06	0.92	1.00	1.00	1.00	1.00	1.00	0.00	0.22	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.07	0.89	1.00	1.00	1.00	1.00	1.00	0.02	0.19	0.77	0.98	1.00	1.00	1.00	1.00
93	0.12	0.55	0.92	0.99	1.00	1.00	1.00	1.00	0.10	0.57	0.94	0.99	1.00	1.00	1.00	1.00	0.06	0.46	0.92	0.99	1.00	1.00	1.00	1.00	--	--	--	--	--	--	--	--
94	0.12	0.61	0.95	1.00	1.00	1.00	1.00	1.00	0.00	0.50	1.00	1.00	1.00	1.00	1.00	1.00	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

TABLE 3. Parameter values and probability for female and male Georges Bank and Gulf of Maine cod estimated from stepwise logistic regressions. Probability values for variables excluded from the model are included.

	Georges Bank Females Lag=2.5		Georges Bank Males Lag=2.5		Gulf of Maine Females Lag=0.0		Gulf of Maine Males Lag=2.5	
	Parameter	Probability	Parameter	Probability	Parameter	Probability	Parameter	Probability
Intercept	-5.9275	0.0001	-6.3968	0.0001	-1.728	0.0643	-2.1669	0.0006
Length	0.1598	0.0001	0.1613	0.0001	0.1046	0.0001	0.081	0.0001
Density	-0.1656	0.0001	-0.137	0.0001	-0.6046	0.0001	-0.4843	0.0001
Temperature	---	0.9746	0.1011	0.0020	---	0.4076	---	0.9533
Length x Density	---	0.1721	---	0.4444	0.0061	0.0425	0.0067	0.0001
Length x Temperature	0.0022	0.0010	---	0.5327	0.0056	0.0467	0.0019	0.0492

TABLE 4a. Predicted mean lengths at age for Georges Bank females, year-classes 1970-1994.

a	b	yc	1	2	3	4	5	6	7	8
10.10	40.20	70	20.65	43.58	58.10	68.74	77.14	84.09	90.01	95.17
6.69	42.49	71	17.84	42.08	57.42	68.67	77.55	84.89	91.15	96.61
6.71	44.51	72	18.39	43.78	59.85	71.63	80.94	88.63	95.19	100.90
7.05	43.00	73	18.33	42.87	58.39	69.77	78.77	86.20	92.53	98.06
8.57	42.46	74	19.71	43.93	59.26	70.50	79.38	86.72	92.97	98.42
7.82	42.95	75	19.09	43.59	59.10	70.46	79.44	86.86	93.19	98.71
3.44	45.48	76	15.38	41.33	57.75	69.79	79.30	87.16	93.86	99.70
10.21	41.44	77	21.08	44.73	59.69	70.66	79.32	86.48	92.59	97.91
16.07	36.86	78	25.74	46.78	60.08	69.84	77.55	83.92	89.35	94.08
15.06	37.21	79	24.82	46.05	59.49	69.33	77.11	83.54	89.03	93.80
13.21	39.59	80	23.60	46.18	60.48	70.95	79.23	86.07	91.91	96.99
15.39	38.81	81	25.58	47.72	61.73	72.00	80.12	86.83	92.54	97.53
17.06	35.49	82	26.38	46.63	59.44	68.83	76.25	82.39	87.62	92.17
6.66	43.35	83	18.03	42.76	58.41	69.88	78.95	86.44	92.82	98.39
19.55	33.83	84	28.42	47.72	59.94	68.89	75.96	81.81	86.79	91.14
16.01	36.48	85	25.58	46.39	59.56	69.22	76.85	83.15	88.53	93.21
11.18	39.57	86	21.56	44.14	58.43	68.90	77.18	84.02	89.85	94.93
12.35	38.73	87	22.51	44.60	58.59	68.84	76.93	83.63	89.33	94.30
13.94	37.42	88	23.76	45.11	58.61	68.52	76.34	82.81	88.32	93.12
16.27	34.19	89	25.24	44.74	57.08	66.13	73.28	79.19	84.23	88.61
13.41	38.39	90	23.48	45.39	59.25	69.41	77.44	84.07	89.73	94.66
13.76	35.76	91	23.14	43.54	56.45	65.92	73.40	79.58	84.85	89.44
0.16	45.02	92	11.98	37.66	53.91	65.83	75.24	83.02	89.65	95.43
12.66	37.54	93	22.51	43.93	57.48	67.42	75.27	81.76	87.29	92.11
16.85	34.86	94	25.99	45.88	58.46	67.69	74.97	81.00	86.13	90.61
min			11.98	37.66	53.91	65.83	73.28	79.19	84.23	88.61
max			28.42	47.72	61.73	72.00	80.94	88.63	95.19	100.90

TABLE 4b. Predicted mean lengths-at-age for Georges Bank males, year-classes 1970-1994.

a	b	yc	1	2	3	4	5	6	7	8
17.03	33.47	70	25.81	44.91	56.99	65.85	72.85	78.64	83.57	87.87
9.31	38.81	71	19.49	41.64	55.65	65.92	74.03	80.74	86.46	91.44
6.17	44.00	72	17.71	42.82	58.70	70.35	79.55	87.15	93.64	99.29
8.99	39.19	73	19.27	41.63	55.78	66.15	74.35	81.12	86.90	91.93
9.14	40.59	74	19.79	42.95	57.60	68.35	76.83	83.85	89.83	95.04
10.11	40.69	75	20.79	44.01	58.69	69.47	77.97	85.01	91.00	96.22
16.22	35.51	76	25.54	45.80	58.62	68.02	75.45	81.59	86.82	91.38
11.95	39.48	77	22.31	44.83	59.09	69.54	77.79	84.61	90.43	95.50
17.30	35.21	78	26.54	46.63	59.34	68.66	76.02	82.11	87.29	91.81
14.17	38.83	79	24.36	46.51	60.53	70.81	78.93	85.64	91.36	96.35
14.56	37.59	80	24.42	45.87	59.44	69.39	77.25	83.75	89.29	94.12
15.78	37.66	81	25.66	47.14	60.74	70.71	78.58	85.09	90.64	95.47
14.90	35.60	82	24.24	44.55	57.40	66.83	74.27	80.42	85.67	90.24
7.53	42.57	83	18.70	42.99	58.35	69.62	78.52	85.88	92.15	97.62
13.11	38.44	84	23.19	45.12	59.00	69.17	77.21	83.85	89.51	94.45
19.17	33.36	85	27.92	46.96	59.00	67.83	74.81	80.57	85.49	89.77
14.29	36.47	86	23.85	44.66	57.83	67.48	75.10	81.41	86.78	91.46
13.74	36.72	87	23.38	44.32	57.58	67.30	74.97	81.32	86.73	91.44
16.31	34.96	88	25.48	45.43	58.06	67.31	74.62	80.66	85.82	90.30
15.94	34.16	89	24.90	44.39	56.72	65.76	72.91	78.81	83.84	88.23
17.60	33.26	90	26.33	45.30	57.30	66.11	73.06	78.81	83.71	87.98
11.29	37.30	91	21.08	42.36	55.82	65.70	73.49	79.94	85.44	90.22
5.79	40.08	92	16.30	39.17	53.64	64.24	72.62	79.55	85.46	90.60
13.23	36.35	93	22.77	43.51	56.64	66.26	73.86	80.14	85.50	90.17
5.20	44.44	94	16.86	42.21	58.26	70.02	79.31	86.99	93.54	99.24
min			16.30	39.17	53.64	64.24	72.62	78.64	83.57	87.87
max			27.92	47.14	60.74	70.81	79.55	87.15	93.64	99.29

TABLE 5a. Predicted mean lengths-at-age for Gulf of Maine females, year-classes 1970-1994.

a	b	yc	1	2	3	4	5	6	7	8
-2.30	42.53	70	8.86	33.12	48.48	59.74	68.63	75.98	82.24	87.70
-12.67	47.51	71	-0.20	26.90	44.06	56.63	66.57	74.78	81.78	87.88
-14.71	50.30	72	-1.51	27.19	45.35	58.66	69.18	77.87	85.28	91.74
-10.98	45.65	73	1.00	27.04	43.52	55.61	65.15	73.04	79.77	85.63
-10.42	47.78	74	2.11	29.37	46.62	59.27	69.26	77.52	84.56	90.70
-5.82	46.83	75	6.46	33.18	50.09	62.48	72.27	80.36	87.26	93.28
-9.46	50.83	76	3.88	32.88	51.23	64.68	75.31	84.09	91.58	98.11
-2.38	46.78	77	9.89	36.58	53.47	65.85	75.64	83.72	90.61	96.62
7.83	37.43	78	17.65	39.00	52.51	62.42	70.25	76.72	82.23	87.03
2.87	42.71	79	14.08	38.45	53.87	65.17	74.10	81.48	87.78	93.26
7.68	38.71	80	17.84	39.93	53.90	64.15	72.25	78.94	84.64	89.61
8.51	37.97	81	18.47	40.14	53.85	63.90	71.84	78.40	84.00	88.87
4.52	40.09	82	15.04	37.92	52.39	63.01	71.39	78.32	84.23	89.37
1.34	43.66	83	12.79	37.70	53.46	65.02	74.15	81.70	88.13	93.73
0.41	41.49	84	11.29	34.97	49.95	60.93	69.60	76.78	82.89	88.22
5.28	37.55	85	15.13	36.56	50.11	60.05	67.90	74.39	79.93	84.75
-4.20	42.79	86	7.02	31.43	46.88	58.20	67.15	74.55	80.85	86.34
-2.28	40.14	87	8.25	31.14	45.63	56.26	64.65	71.59	77.50	82.65
-6.68	47.21	88	5.71	32.64	49.69	62.18	72.06	80.22	87.17	93.23
-0.82	39.29	89	9.49	31.91	46.09	56.50	64.71	71.50	77.29	82.34
0.81	42.07	90	11.85	35.85	51.03	62.17	70.96	78.23	84.43	89.83
0.77	38.45	91	10.86	32.80	46.68	56.86	64.90	71.55	77.21	82.15
0.33	37.97	92	10.29	31.95	45.66	55.70	63.64	70.21	75.80	80.67
13.91	33.18	93	22.62	41.55	53.52	62.31	69.24	74.98	79.86	84.12
16.60	26.93	94	23.66	39.02	48.74	55.87	61.50	66.16	70.12	73.58
min			-1.51	26.90	43.52	55.61	61.50	66.16	70.12	73.58
max			23.66	41.55	53.90	65.85	75.64	84.09	91.58	98.11

TABLE 5b. Predicted mean lengths-at-age for Gulf of Maine males, year-classes 1970-1994.

a	b	yc	1	2	3	4	5	6	7	8
-3.05	41.02	70	7.72	31.12	45.93	56.79	65.37	72.46	78.51	83.77
-9.38	43.97	71	2.16	27.24	43.12	54.76	63.95	71.55	78.03	83.68
-11.87	46.24	72	0.26	26.64	43.34	55.58	65.25	73.24	80.05	85.99
-9.19	43.28	73	2.17	26.86	42.48	53.94	62.99	70.47	76.85	82.40
-5.99	44.52	74	5.69	31.09	47.16	58.95	68.26	75.95	82.51	88.23
-2.07	42.90	75	9.19	33.67	49.15	60.51	69.48	76.89	83.21	88.72
-0.39	46.47	76	11.80	38.32	55.09	67.39	77.11	85.14	91.99	97.96
-1.24	45.81	77	10.78	36.92	53.45	65.58	75.16	83.08	89.82	95.71
9.10	35.60	78	18.44	38.75	51.60	61.03	68.47	74.62	79.87	84.44
8.62	38.84	79	18.81	40.97	54.99	65.27	73.39	80.10	85.83	90.81
6.01	39.66	80	16.42	39.05	53.37	63.87	72.16	79.02	84.86	89.95
10.08	36.50	81	19.66	40.49	53.66	63.33	70.96	77.27	82.65	87.33
11.04	35.80	82	20.43	40.85	53.78	63.25	70.74	76.93	82.20	86.80
1.03	44.46	83	12.70	38.07	54.12	65.89	75.19	82.87	89.42	95.13
0.75	39.26	84	11.05	33.45	47.62	58.02	66.22	73.01	78.79	83.83
5.95	36.37	85	15.50	36.24	49.37	59.00	66.60	72.89	78.24	82.91
2.29	35.93	86	11.72	32.22	45.19	54.70	62.21	68.42	73.72	78.33
-0.70	37.64	87	9.17	30.65	44.23	54.20	62.06	68.57	74.11	78.95
7.68	33.61	88	16.50	35.67	47.81	56.70	63.73	69.54	74.49	78.81
6.62	34.77	89	15.74	35.58	48.13	57.33	64.60	70.61	75.74	80.20
5.08	37.94	90	15.04	36.68	50.38	60.42	68.36	74.92	80.51	85.38
6.63	33.77	91	15.49	34.76	46.95	55.89	62.96	68.79	73.77	78.10
1.82	36.21	92	11.32	31.98	45.05	54.64	62.21	68.47	73.80	78.45
0.99	43.15	93	12.31	36.93	52.50	63.92	72.95	80.40	86.76	92.30
0.48	41.43	94	11.35	34.99	49.94	60.91	69.57	76.73	82.83	88.15
min			0.26	26.64	42.48	53.94	62.06	68.42	73.72	78.10
max			20.43	40.97	55.09	67.39	77.11	85.14	91.99	97.96

TABLE 6. Parameter estimates and probability from regression of predicted mean length over the time series for year-classes 1970-1989.

	Georges Bank				Gulf of Maine			
	females		males		females		males	
	parameter	probability	parameter	probability	parameter	probability	parameter	probability
age 1	0.3665	0.005	0.2301	0.0404	0.4687	0.0469	0.6512	0.0036
age 2	0.1433	0.0394	0.1152	0.069	0.2514	0.1368	0.3392	0.0629
age 3	0.002	0.9644	0.0424	0.4343	0.1137	0.421	0.1416	0.4139
age 4	-0.1015	0.0389	-0.0111	0.8654	0.013	0.9225	-0.0032	0.9858
age 5	-0.1833	0.0046	-0.0531	0.5158	-0.0667	0.6271	-0.1178	0.5278
age 6	-0.2507	0.002	-0.0883	0.3655	-0.1323	0.3648	-0.2121	0.2833
age 7	-0.3084	0.0014	-0.1179	0.2923	-0.1884	0.2298	-0.2928	0.1619
age 8	-0.3591	0.0012	-0.1438	0.2499	-0.2375	0.1587	-0.363	0.1002

TABLE 7. Parameter values and tests for significance of intercepts and slopes from analysis of covariance for Georges Bank and Gulf of Maine female and male Atlantic cod, year-classes 1970-1994. (n = number of observations, ns=not significant, * = significant at p = 0.05, ** = significant at p = 0.01)

Georges Bank									Gulf of Maine							
Year-class	n Male	Intercept Female		Male	Slope Female		Male		Year-class	n	Intercept Female		Male	Slope Females		
1970	390	10.10	ns	17.03	40.20	**	33.47		1970	213	-2.30	*	-3.05	42.53	ns	41.02
1971	1646	6.69	**	9.31	42.49	**	38.81		1971	1057	-12.67	**	-9.38	47.51	*	43.97
1972	474	6.71	ns	6.17	44.51	ns	44.00		1972	121	-14.71	ns	-11.87	50.30	ns	46.24
1973	293	7.05	**	8.99	43.00	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	7.82	ns	10.11	42.95	*	40.69		1975	323	-5.82	ns	-2.07	46.83	ns	42.90
1976	107	3.44	ns	16.22	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	17.30	36.86	ns	35.21		1978	282	7.83	ns	9.10	37.43	ns	35.60
1979	393	15.06	ns	14.17	37.21	ns	38.83		1979	197	2.87	ns	8.62	42.71	ns	38.84
1980	975	13.21	ns	14.56	39.59	*	37.59		1980	311	7.68	ns	6.01	38.71	ns	39.66
1981	508	15.39	ns	15.78	38.81	ns	37.66		1981	228	8.51	ns	10.08	37.97	ns	36.50
1982	221	17.06	ns	14.90	35.49	ns	35.60		1982	208	4.52	ns	11.04	40.09	ns	35.80
1983	609	6.66	ns	7.53	43.35	ns	42.57		1983	250	1.34	ns	1.03	43.66	ns	44.46
1984	182	19.55	ns	13.11	33.83	ns	38.44		1984	207	0.41	ns	0.75	41.49	ns	39.26
1985	923	16.01	ns	19.17	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	36.47		1986	388	-4.20	ns*	2.29	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	13.94	ns	16.31	37.42	ns	34.96		1988	84	-6.68	ns	7.68	47.21	*	33.61
1989	220	16.27	ns	15.94	34.19	ns	34.16		1989	77	-0.82	ns	6.62	39.29	ns	34.77
1990	486	13.41	ns	17.60	38.39	**	33.26		1990	172	0.81	ns	5.08	42.07	ns	37.94
1991	224	13.76	ns	11.29	35.76	ns	37.30		1991	250	0.77	ns	6.63	38.45	ns	33.77
1992	339	0.16	ns	5.79	45.02	*	40.08		1992	353	0.33	ns	1.82	37.97	ns	36.21
1993	327	12.66	ns	13.23	37.54	ns	36.35		1993	98	13.91	ns	0.99	33.18	ns	43.15
1994	119	16.85	ns	5.20	34.86	*	44.44		1994	69	16.60	ns	0.48	26.93	*	41.43
1995	206	19.95	ns	15.97	28.70	ns	33.74		1995	25	18.29	ns	18.31	22.30	ns	22.61
1996	109	17.82	ns	20.13	30.59	ns	26.78		1996	21	16.97	ns	18.41	15.36	ns	11.44

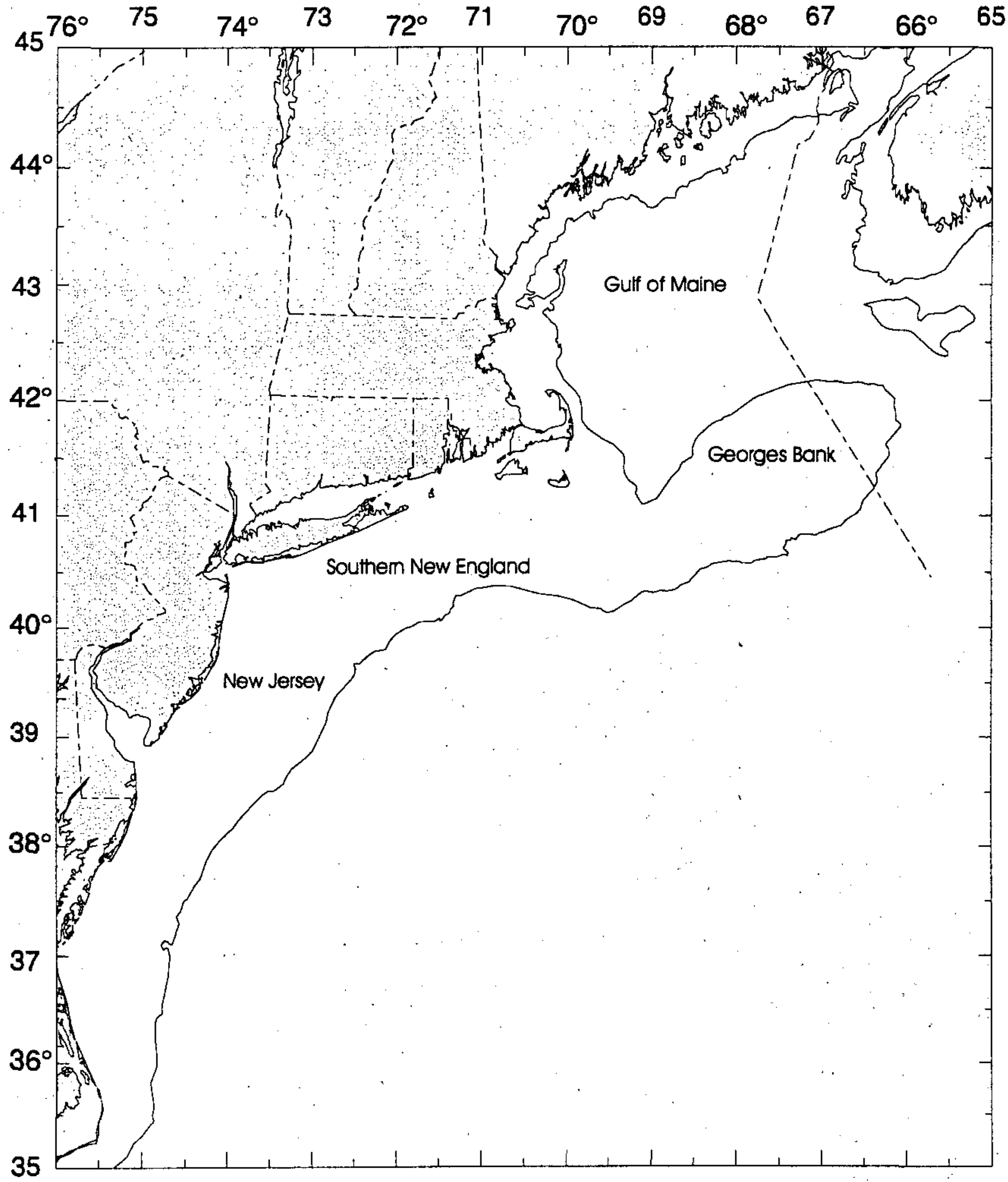


Figure 1. The Gulf of Maine, Georges Bank, Southern New England, and coastal New Jersey Atlantic cod stocks as defined by Wise (1963).

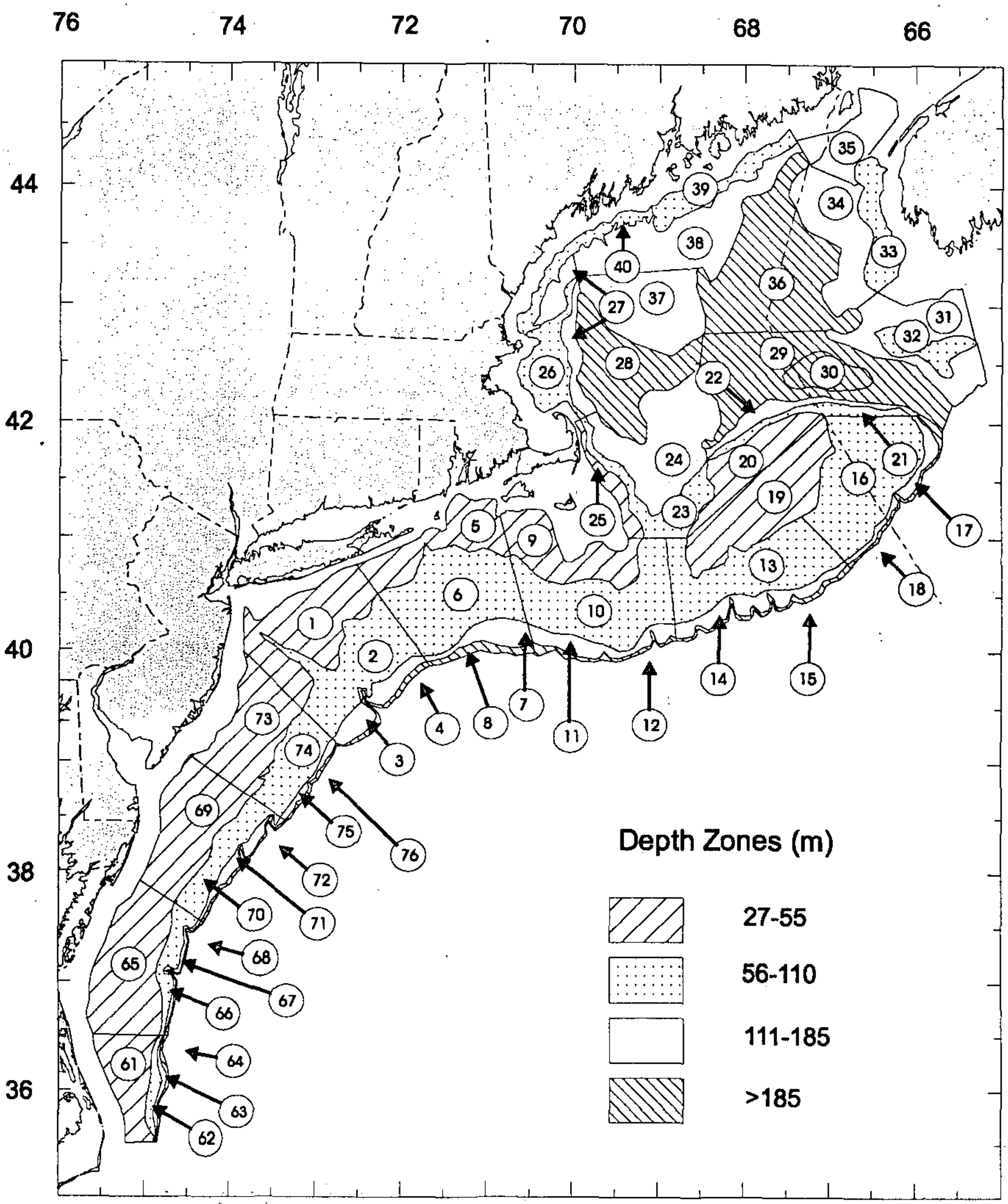


Figure 2. NEFSC offshore bottom trawl survey strata in the Northwest Atlantic.

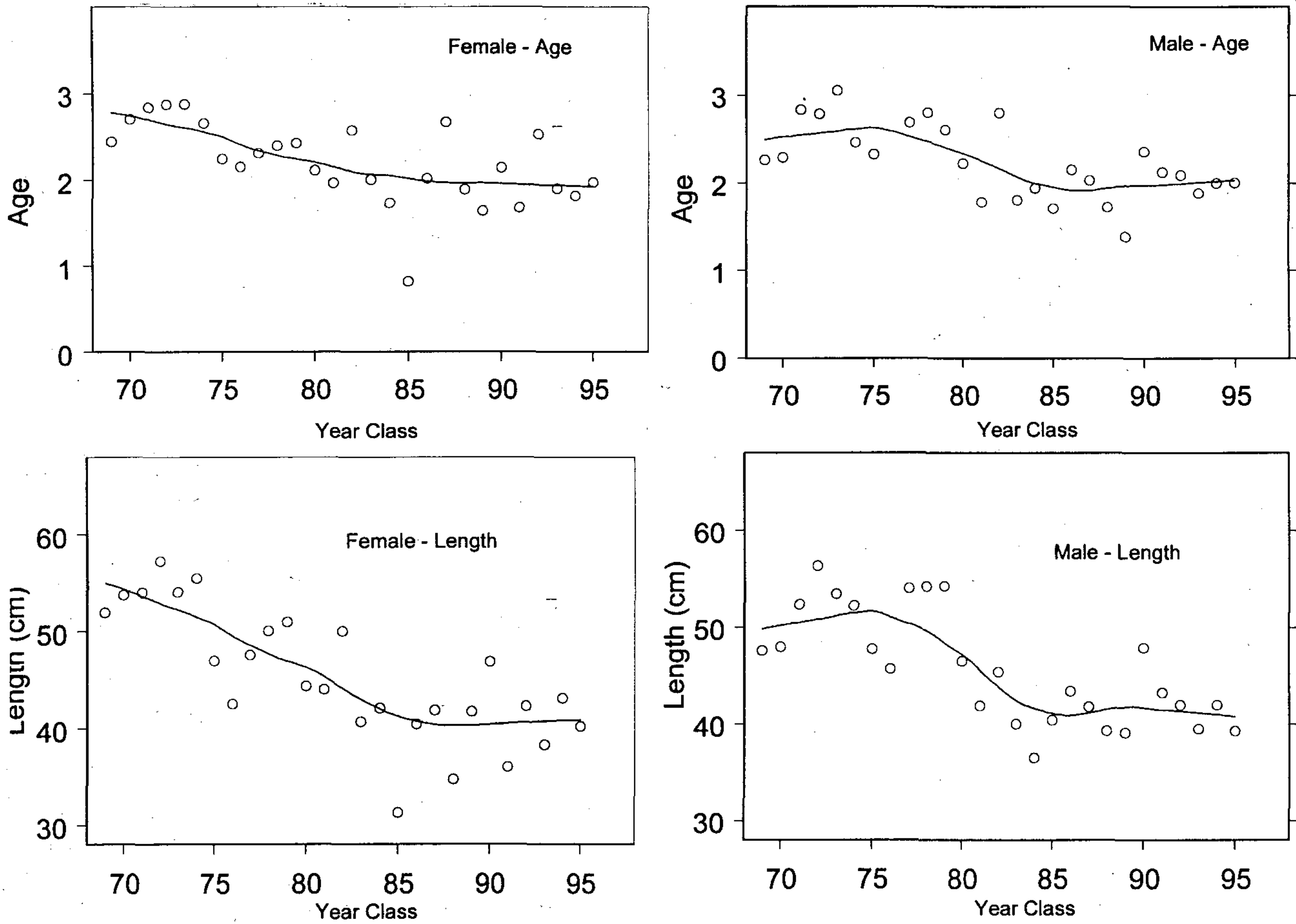


Figure 3. Median age and length at maturity by year class for female and male Atlantic cod from Georges Bank.

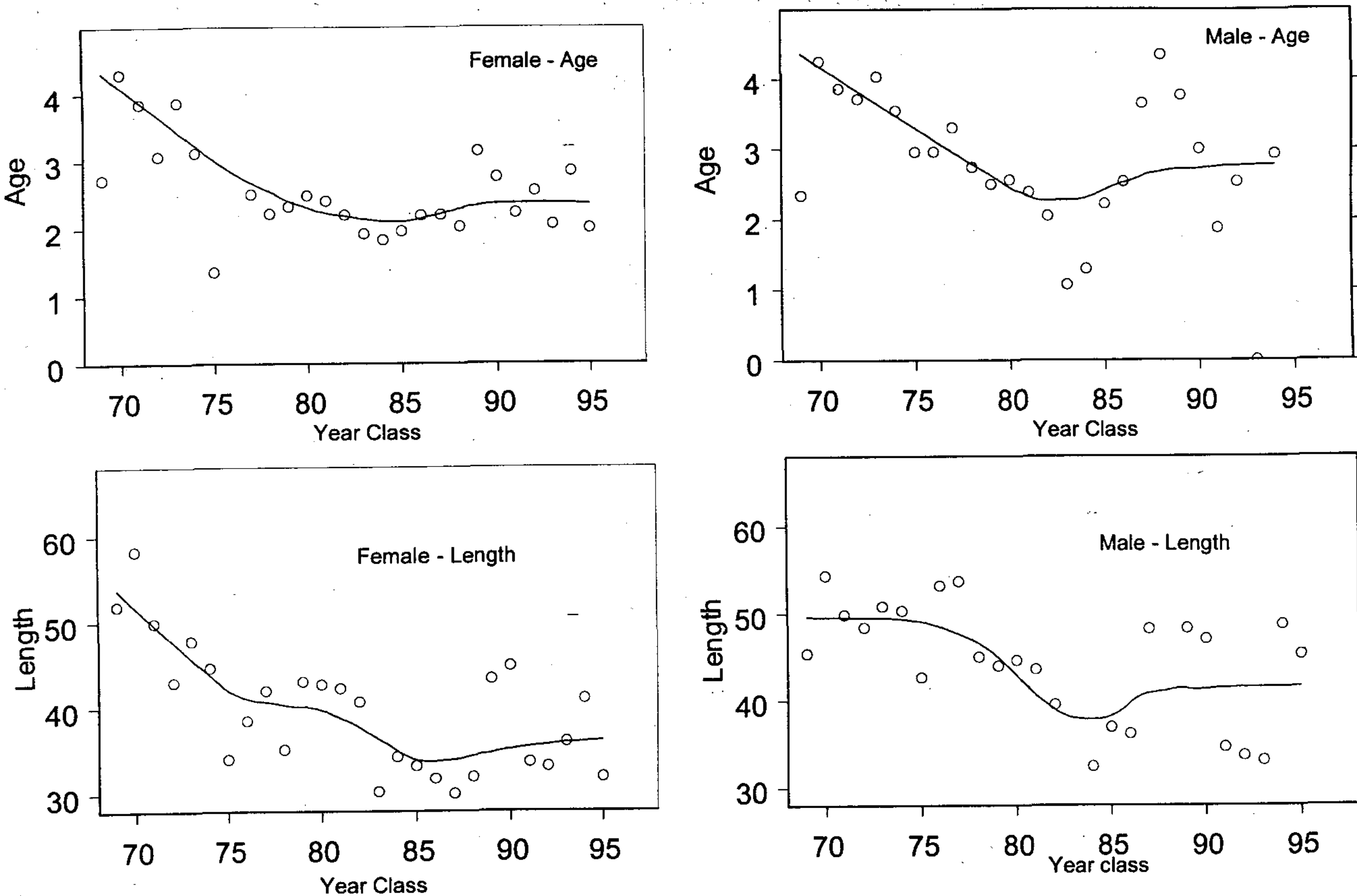


Figure 4. Median age and length at maturity by year class for female and male Atlantic cod from the Gulf of Maine.

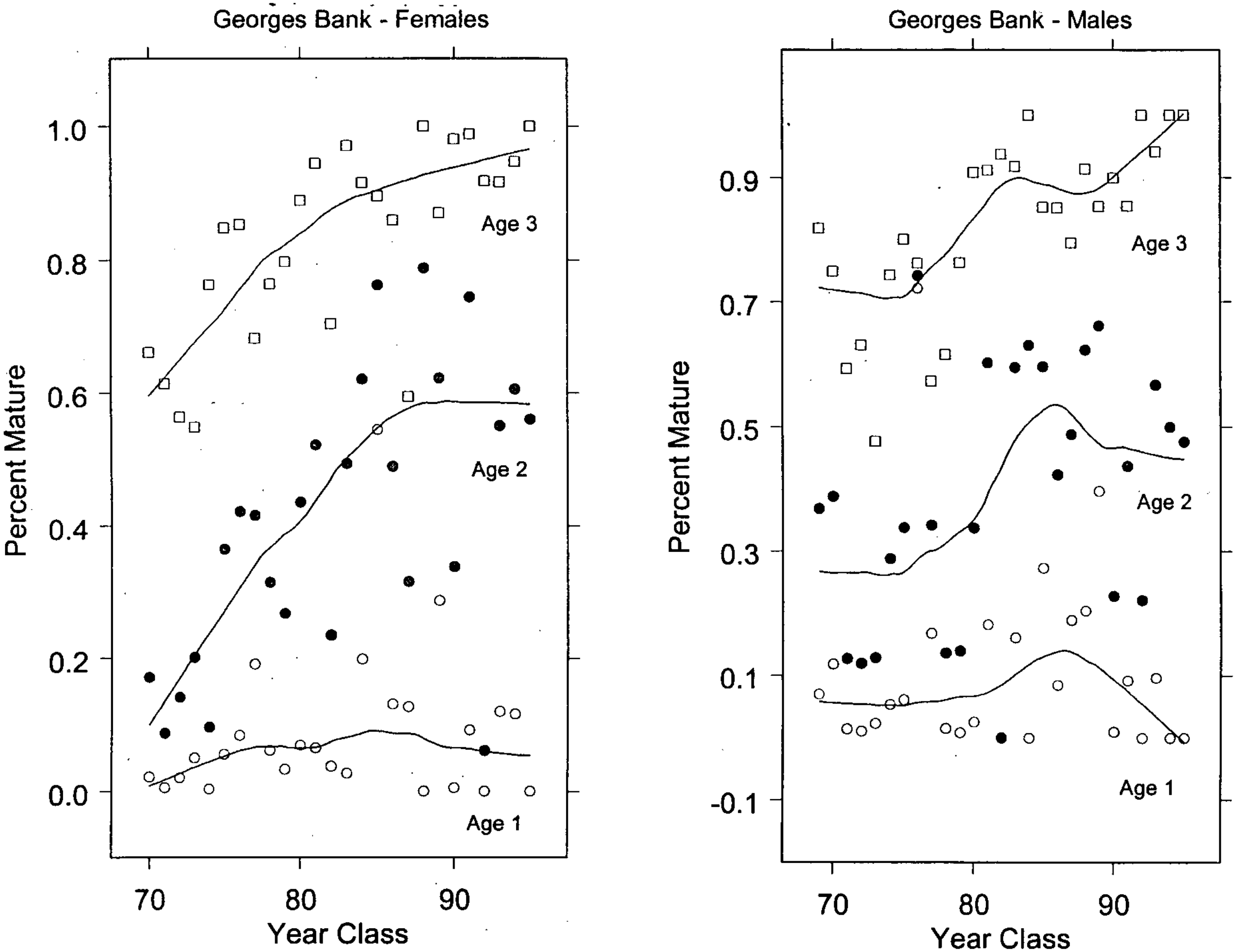


Figure 5. Percent mature at age by year class for ages 1, 2, and 3 for female and male cod from Georges Bank.

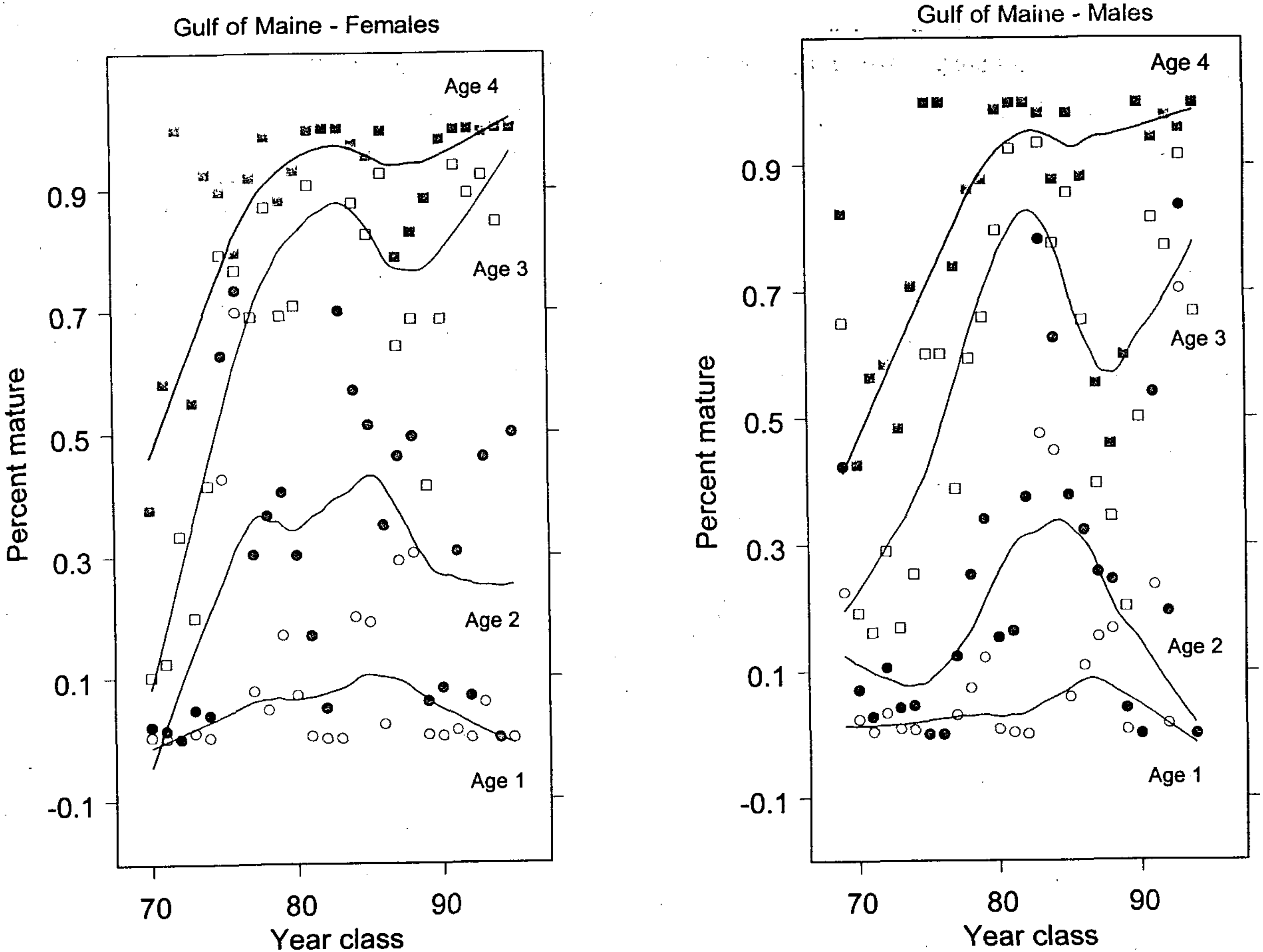


Figure 6. Percent mature at age by year class for ages 1, 2, 3, and 4 for female and male cod from the Gulf of Maine.

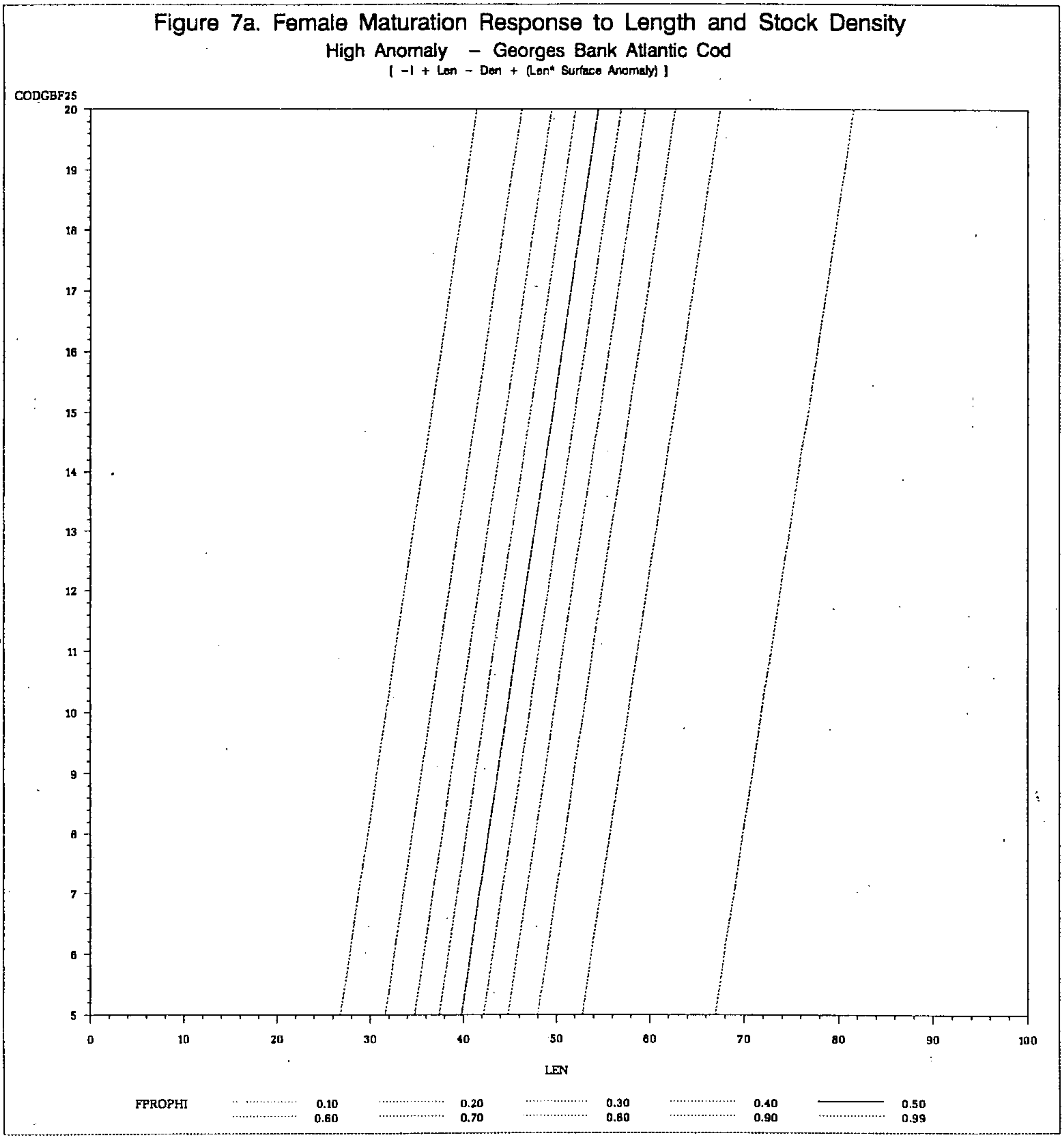


Figure 7a. Female Maturation Response to Length and Stock Density
High Anomaly – Georges Bank Atlantic Cod
[-I + Len - Den + (Len* Surface Anomaly)]
CODGBF25
LEN
FPROPHI
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
0.99

Figure 7b. Female Maturation Response to Length and Stock Density

Low Anomaly – Georges Bank Atlantic Cod

[–I + Len – Den + (Len * Surface Anomaly)]

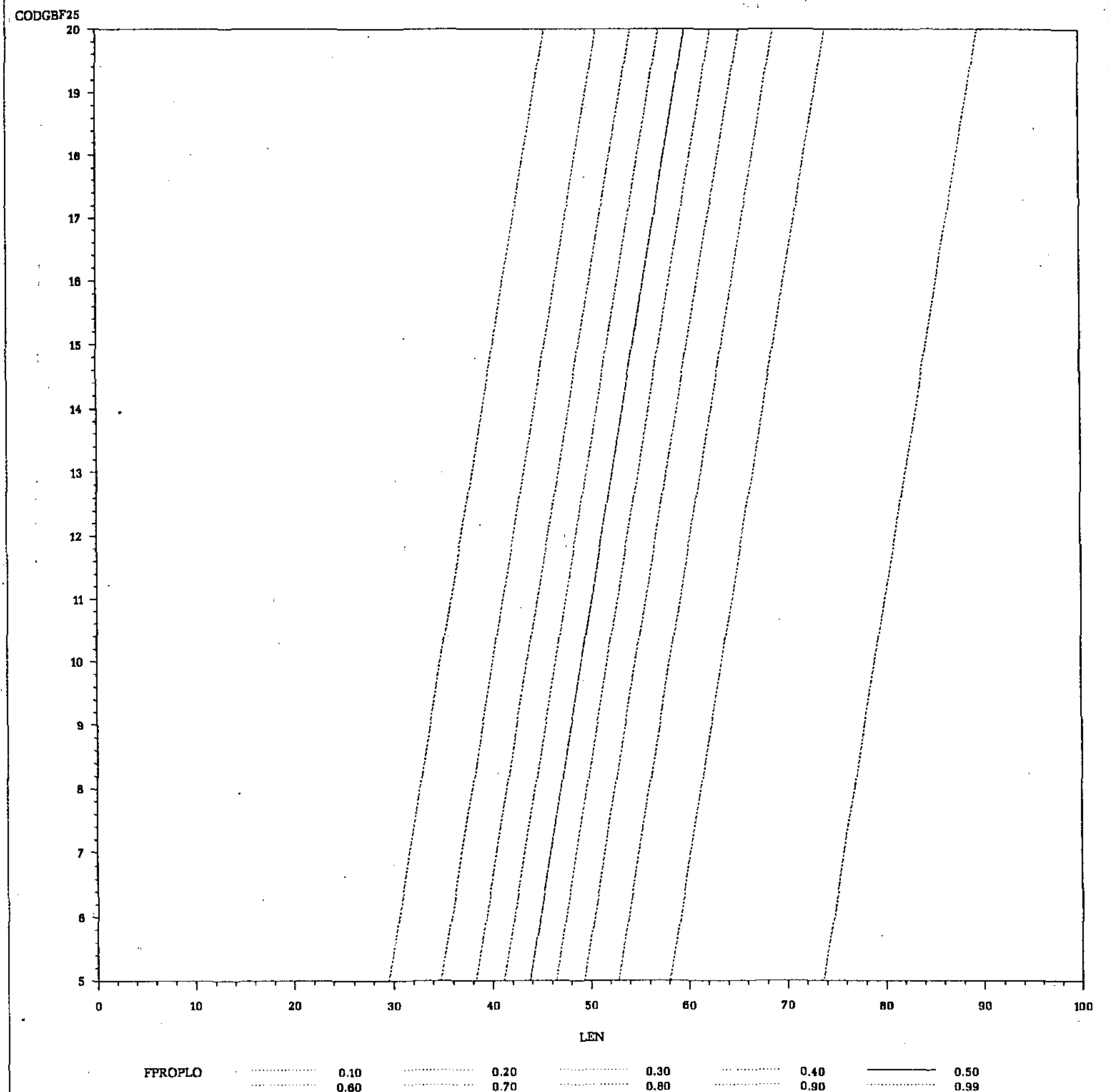


Figure 8a. Female Maturation Response to Length and Stock Density

High Anomaly – Gulf of Maine Atlantic Cod

[–I + Len – Den + (Len*Den) + (Len*Surface Anomaly)]

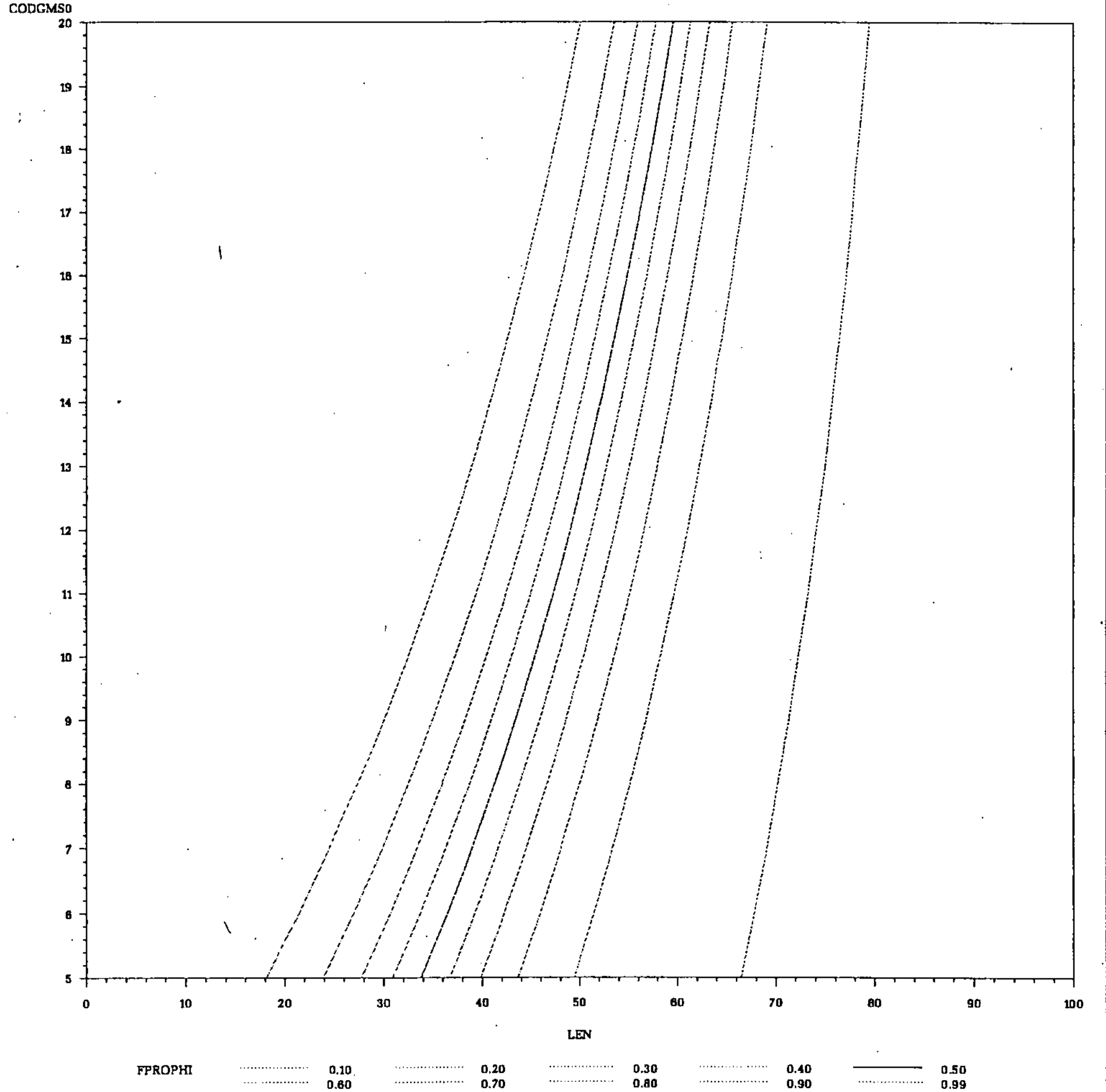
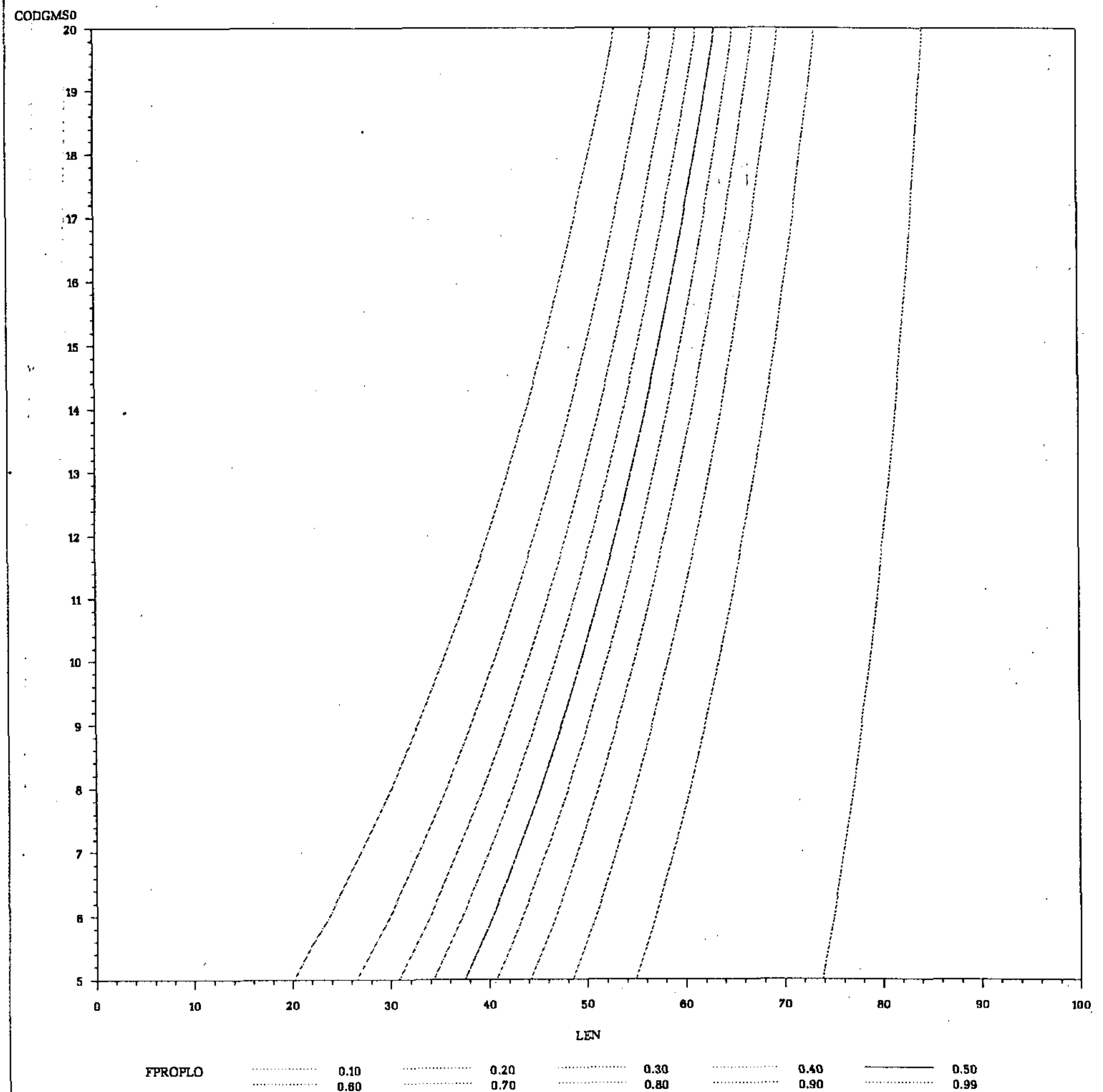


Figure 8b. Female Maturation Response to Length and Stock Density

Low Anomaly – Gulf of Maine Atlantic Cod

[–I + Len – Den + (Len*Den) + (Len*Surface Anomaly)]



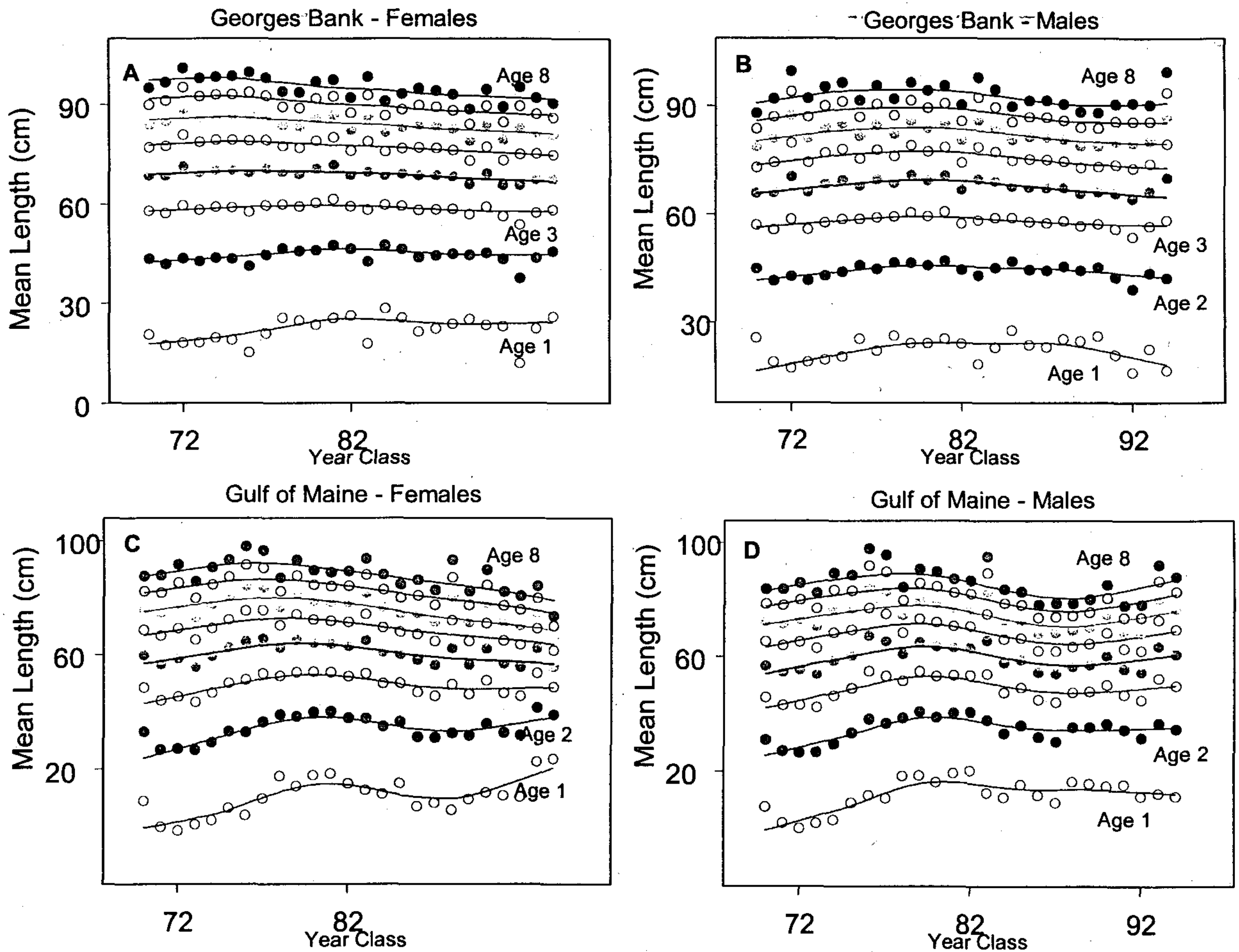


Figure 9. Predicted mean length at age by year class for ages 1-8 for females and males from Georges Bank and the Gulf of Maine.

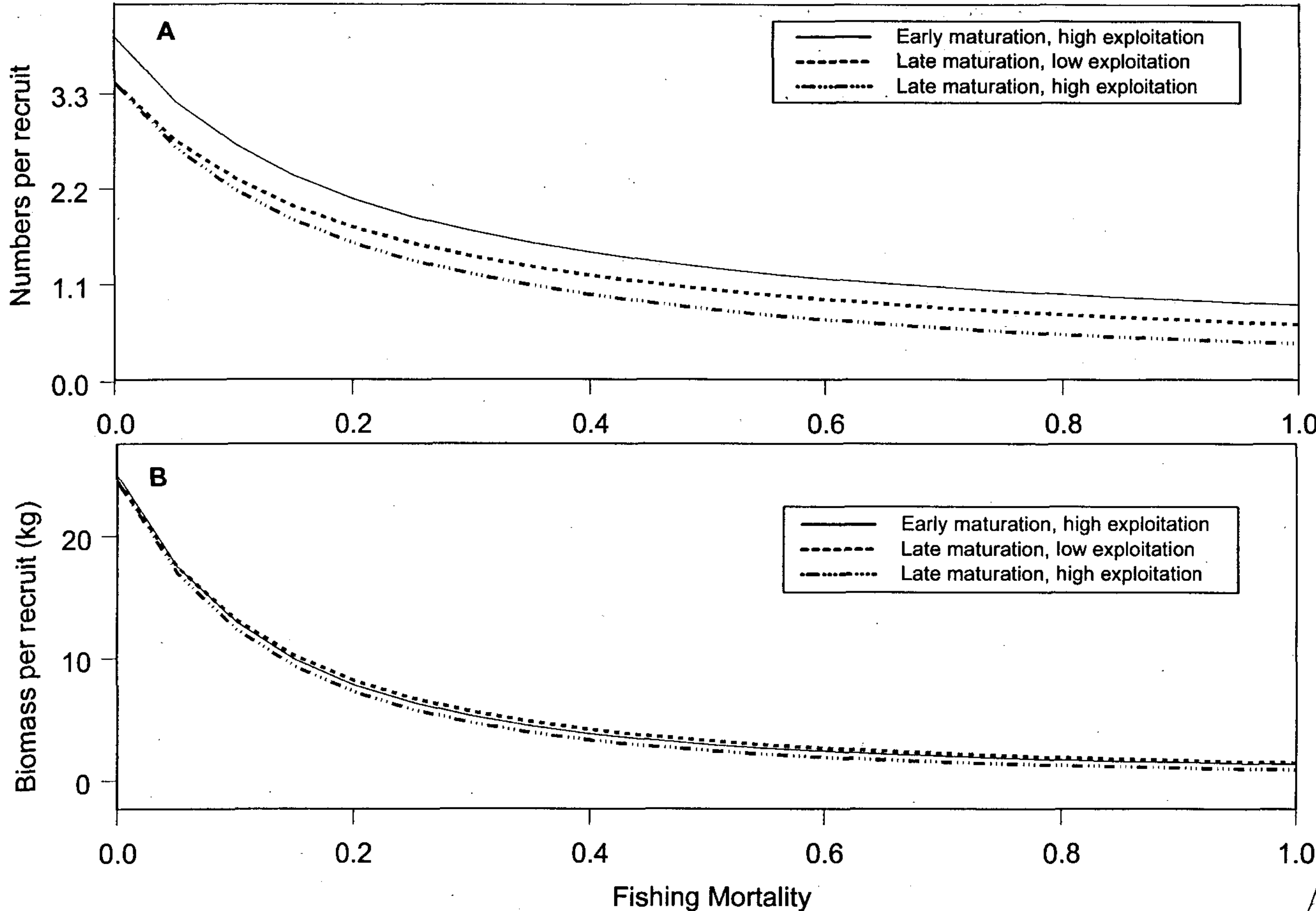


Figure 10. Spawning stock numbers (A) and biomass (B) per recruit for three scenarios of maturation and exploitation for fishing mortality from 0.0 to 1.0 for Georges Bank female Atlantic cod.