Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered

Caihong Fu, Robert Mohn, and L. Paul Fanning

Abstract: An age-structured population dynamics model, incorporating interactions between Atlantic cod (*Gadus morhua*), the fishery, and the grey seal (*Halichoerus grypus*) population, was applied to the cod stock off eastern Nova Scotia (Northwest Atlantic Fisheries Organization Divisions 4Vs and 4W, commonly abbreviated to 4VsW), a stock that has dramatically declined since the late 1980s. Mortality was modeled as having three components: fishing mortality (F), seal predation (M^p), and all other sources of natural mortality (M). Specifically, M was assumed to be distinct for immature cod (ages 1–4; M^i) and mature cod (age 5 and older; M^m), and respective annual variations were estimated. Parameters estimated also included recruitment (cod abundance at age 1; R), F, and M^p. Based on our estimates of F, M^p, and M, it is unlikely that the collapse of the 4VsW cod stock can be attributed to a sudden increase in M; fishing appears to have been the primary cause for the stock's decline. However, after the moratorium on commercial fishing in 1993, increasing M^p and M^m and low R may have contributed to the failure of the 4VsW cod stock to recover.

Résumé : Un modèle de dynamique de population basé sur les structures d'âges qui incorpore les interactions entre la Morue franche (*Gadus morhua*), les pêches commerciales et la population de Phoques gris (*Halichoerus grypus*) a été appliqué au stock de morues du large de la côte est de la Nouvelle-Écosse (divisions 4VsW de l'Organisation des pêches de l'Atlantique nord-ouest), un stock qui a chuté de façon dramatique depuis la fin des années 1980. La modélisation de la mortalité a trois composantes, la mortalité due à la pêche (F), la prédation par les phoques (M^p) et les autres sources de mortalité naturelle (M). Plus précisément, une mortalité distincte est attribuée aux morues immatures (âges 1–4, M^i) et matures (âges 5 et plus, M^m) et, pour chacune, les variations annuelles sont estimées. Les variables, comme le recrutement (R, abondance des morues à l'âge 1), F et M^p, sont aussi estimées. D'après nos estimations de F, M^p et M, il est peu probable que le déclin du stock 4VsW soit attribuable à une augmentation soudaine de M; les pêches commerciales semblent avoir été la cause principale de la chute du stock. Toutefois, après le moratoire sur les pêches commerciales en 1993, des valeurs croissantes de M^p et de M^m et un R faible peuvent avoir contribué à l'incapacité du stock 4VsW de se rétablir.

[Traduit par la Rédaction]

Introduction

Six Canadian stocks of Atlantic cod (*Gadus morhua*) ranging from southern Labrador to the continental shelf off eastern Nova Scotia collapsed almost simultaneously to the point where moratoria on commercial exploitation were declared in 1992 and 1993 (Myers et al. 1996). The reasons for these collapses were unknown, and were the subject of considerable debate. Some linked stock declines to natural causes and others to fishing activities. The ongoing debate over many other collapsed species across many jurisdictions underscores the difficulties of unambiguously demonstrating the relative influences of environmental, ecosystem, and fishing effects on heavily exploited species (Frank et al. 1996).

For the six cod stocks off eastern Canada, recruitment of year-classes that should have contributed most to the spawning stock at the time of collapses was found not to differ from recruitment levels in earlier years (Myers et al. 1997). High fishing mortality was identified as the primary cause for these collapses (Hutchings and Myers 1994; Myers and Cadigan 1995; Myers et al. 1996). On the other hand, Rose et al. (2000) argues that the collapses cannot be attributed in total to fisheries. Major environmental changes took place during the period of cod decline (Drinkwater and Mountain 1997), which may have led to the shift of cod distribution (Rose et al. 2000), reduced recruitment (deYoung and Rose 1993), and increased vulnerability to overfishing (Rose and Kulka 1999).

It was also suggested that body condition factors for cod in the northern Gulf of St. Lawrence declined throughout the early 1990s (Lambert and Dutil 1997), owing to poor environmental conditions (Dutil et al. 1999). The reduced condition of cod may have led to an increase in natural mortality, particularly for adults that have to invest energy reserves in reproduction (Lambert and Dutil 2000; Dutil and Lambert 2000). Diagnostic analysis of commercial catch and research-survey data obtained from the cod stock off southern

C. Fu,[1,2] R. Mohn, and L.P. Fanning. Department of Fisheries and Oceans, Bedford Institute of Oceanography, Marine Fish Division, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

[1]Corresponding author (e-mail: FuC@dfo-mpo.gc.ca).

[2]Present address: Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6.

1614

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

Labrador and eastern Newfoundland suggested that large amounts of the 1987 year-class died as 4-year-olds in 1991 and as 5-year-olds in 1992 (Shelton and Lilly 2000). Although Myers and Cadigan (1995) rejected the hypothesis for the same cod stock that natural mortality increased in 1991, the increasing divergence of recruitment between research-survey analysis and virtual population analysis suggested increased losses of fish (Myers et al. 1997). Myers et al. (1997) attributed the losses to increased misreporting and discarding of catches of young. However, the quantity of missing fish in relation to the capacity of fishery at that time suggested that additional factors such as an increase in natural mortality due to reduced condition also played a role (Shelton and Lilly 2000). In addition, increased predation by seals may also have contributed to the collapse (Mohn and Bowen 1996).

In the case of each of the six collapsed cod stocks off eastern Canada, we may never be able to determine the relative importance of environmental changes (including predation) and fishing activities in the population changes. Nevertheless, there is little doubt that the sequential population analysis (SPA) which failed to provide acceptable population reconstruction during the time of population decline (Mohn 1999; Shelton and Lilly 2000) must have violated one or more of the model assumptions, such as constant natural mortality, accurate catch data, or constant research-survey catchability (Shelton and Lilly 2000). Thus, the most important question in stock assessment and fisheries management at this point is how to develop more realistic population models that require fewer and less rigid assumptions. This paper presents a modelling exercise intended to shed light on what may have happened to the cod stock off eastern Nova Scotia in Northwest Atlantic Fisheries Organization Divisions 4Vs and 4W (Fig. 1), commonly abbreviated to 4VsW.

The cod stock in 4VsW has been managed as one unit, although there is evidence that the cod stock in 4VsW comprises separate substocks (reviewed in Halliday and Pinhorn 1990). Before 1993, the stock was an important commercial resource. Catches averaged 49 600 (ranging from 10 000 to 80 000) metric tonnes (t) annually (Mohn et al. 1998). In 1992, the total catch reached 29 805 t under a total allowable catch (TAC) of 35 200 t. In 1993, the TAC was reduced to 11 000 t, in part because of the shortfall in 1992. Landings in 1993 amounted to 3474 t (Mohn et al. 1998), again considerably lower than the TAC. Population abundance of 4VsW cod appeared to have declined rapidly during 1993. The directed fishery for 4VsW cod was closed in September 1993, and abundance not only has remained low but has continued to decline since then.

Stock assessments of 4VsW cod have been undertaken routinely since 1975 (Halliday 1975). Stock assessments made before 1997 were based on SPA, assuming constant natural mortality of 0.2 over age and time (Fanning et al. 1996). However, there were concerns about the retrospective pattern in parameter estimates of population biomass and fishing mortality, i.e., the estimates deviated systematically as data were annually eliminated from or added to the assessment (Mohn 1999). Owing to the strong retrospective pattern, the most recent assessment was revised by assuming that natural mortality increased from 0.2 to 0.4 after 1985. In

addition, predation by grey seals (*Halichoerus grypus*) was explicitly incorporated into the model because of increasing concern about removals attributed to seals (Mohn et al. 1998). These adjustments resulted in the retrospective pattern being greatly reduced, but its causes for the most part remained unknown. Also unresolved was what caused the population to decline, and whether consumption by seals had played an important role in cod population dynamics.

This paper develops a model based on a framework of interactions between cod, fisheries, and seals in which annual variations in natural mortality for both immature (ages 1–4) and mature cod (age 5 and older) were estimated explicitly. In addition, more parameter uncertainties were incorporated, including those in gear selectivity. The goal of this paper is to use this model to estimate time-varying mortality parameters and recruitment, to give a better rationale for the decline of the 4VsW cod stock and especially its failure to recover.

Methods

Data

Data used in the present work include catch at age from commercial fishery ($\tilde{C}_{t,a}$), exploitable number at age estimated from July research surveys ($\tilde{N}_{t,a}$), number at age consumed by grey seals ($\tilde{C}_{t,a}^{\mathrm{p}}$) estimated according to Mohn and Bowen (1996), and cod weight at age estimated from commercial-fishery samples (W_a). Index t is for the years 1970–1997 and index a for ages from 1 to maximum age, A. The maximum age, A, was set at 12 to avoid many zeros in the data. There are two sets of estimated seal-consumption data, $\tilde{C}_{t,a}^{\mathrm{p}}$, depending on the assumption of cod fraction in the diet of grey seals (Mohn and Bowen 1996). When the cod fraction in the seal diet is assumed to be constant, calculation of $\tilde{C}_{t,a}^{\mathrm{p}}$ is independent of the size of the cod stock. If cod fraction is assumed to be proportional to cod-stock size, then the calculation of $\tilde{C}_{t,a}^{\mathrm{p}}$ needs to be updated when the cod-stock size changes.

Population model

An age-structured separable model was constructed for the 4VsW cod stock. Because it is more convenient and easier to estimate a time series of parameters by estimating their deviations from a mean value (Otter Research Ltd. 1998), annual recruitment (R) at age 1 was modeled as $\ln(R_t) = \ln(\overline{R}) + \eta_t^R$, where $\overline{R}$ is the assumed average level set at 12 million and η_t^R is the deviation term. Similarly, instantaneous fishing mortality (F) of fully selected cod was modeled as $\ln(F_t) = \ln(\overline{F}) + \eta_t^F$ with $\overline{F}$ being set at 0.4. Cod age-classes were separated into two groups according to their maturity, following Mohn et al. (1998), where it was assumed that immature cod were aged 1–4 and mature cod were aged 5 and older. Natural mortality (M) was assumed to be distinct for immature cod (M^{i}) and mature cod (M^{m}). Mortalities M^{i} and M^{m} and predation mortality (M^{p}) were modeled as the time-series structure of a random walk: $\ln(M_{t+1}^{\mathrm{i}}) = \ln(M_t^{\mathrm{i}}) + \eta_t^{\mathrm{i}}$, $\ln(M_{t+1}^{\mathrm{m}}) = \ln(M_t^{\mathrm{m}}) + \eta_t^{\mathrm{m}}$, and $\ln(M_{t+1}^{\mathrm{p}}) = \ln(M_t^{\mathrm{p}}) + \eta_t^{\mathrm{p}}$ where η_t^{i}, η_t^{m}, and η_t^{p} are the deviation terms.

Selectivity for the research-survey gear at age a was modeled as a logistic curve $s_a^{\mathrm{s}} = \dfrac{1}{1 + \mathrm{e}^{-\gamma^{\mathrm{s}}(a - \delta^{\mathrm{s}})}}$. Parameters γ^{s}, the shape parameter, and δ^{s}, the age at which 50% of the individuals are vulnerable to research-survey gear, were assumed to be time-independent. Gear selectivity for commercial fishing was modeled as three distinct logistic curves based on changes in the regulated trawl gear

Fig. 1. Map showing the location of Northwest Atlantic Fisheries Organization Divisions 4VsW off eastern Nova Scotia, Canada.
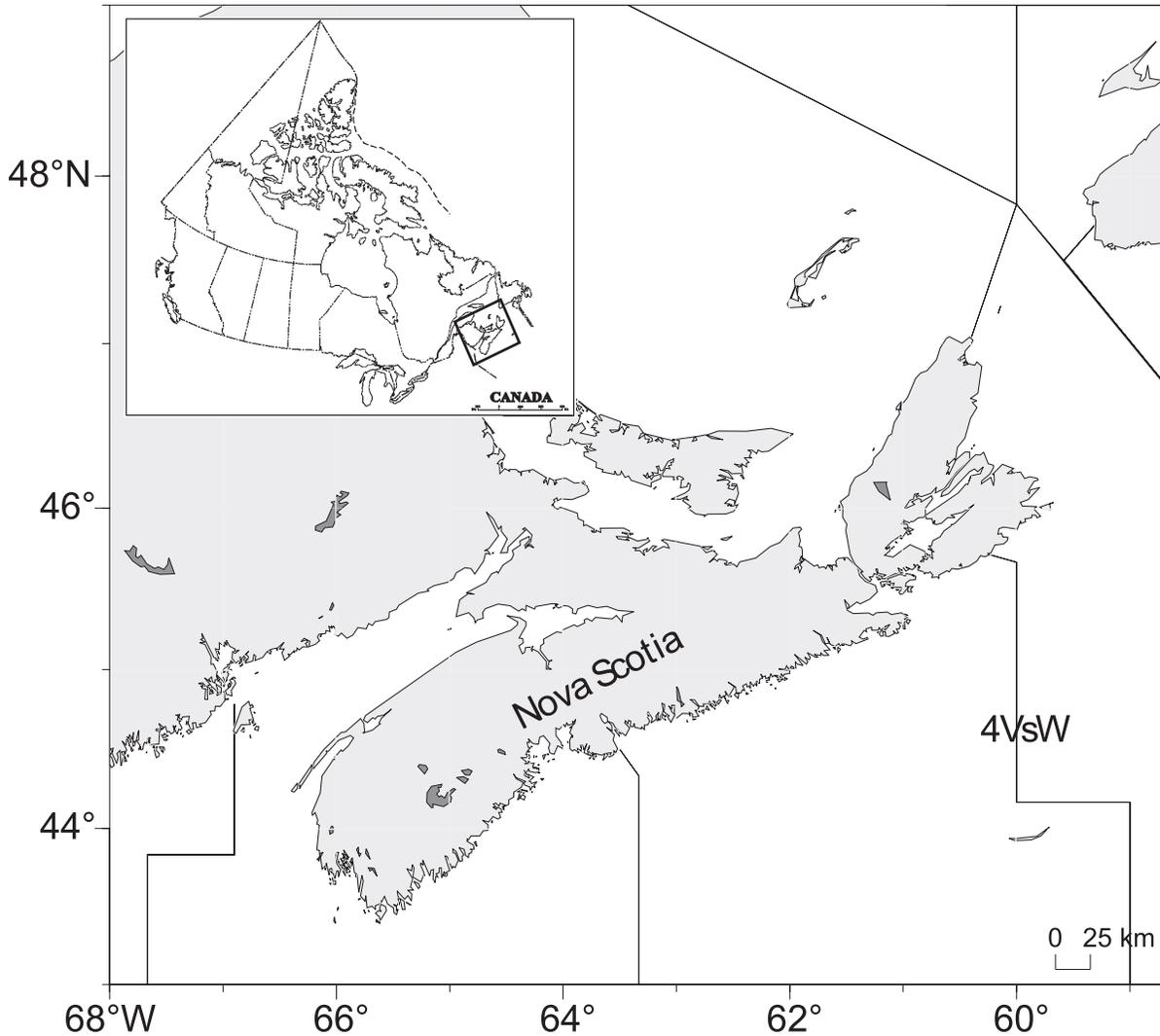
mesh size over the fishing history: $s_a^{C_k} = \dfrac{1}{1 + e^{-\gamma^{C_k}(a - \delta^{C_k})}}$, with $k = 1$ for the period 1970–1976, $k = 2$ for 1977–1982, and $k = 3$ for 1983–1997. Predation selectivity was modeled as a descending logistic curve: $s_a^p = \dfrac{1}{1 + e^{\gamma^p(a - \delta^p)}}$ for ages 2–7. With age 1 cod, selectivity, s_1^p, was estimated individually to eliminate the pattern of consistently positive residuals of numbers of age 1 cod consumed. Predation selection, s_a^p, is assumed to be 0.0 for age 8 and older, based on seal-diet data.

The expected number of age 1 cod in year 1970 was calculated as $N_{1970,a} = \overline{R}e^{\eta_{1970}^R}$. For ages above 1, $N_{1970,a} = \overline{R}e^{\eta_{1970-a+1}^R} \prod_a e^{-\overline{M}}$.

Natural mortality during the initial period of $A - 1$ years before 1970, $\overline{M}$, was assumed to be constant at 0.2 because it has little effect on the estimation of other parameters (Fu and Quinn 2000). Expected numbers at age a in subsequent years are

$$N_{t,a} = N_{t-1,a-1}e^{-Z_{t-1,a-1}},\ 1 < a < A - 1,$$

and

$$N_{t,A^+} = N_{t-1,A-1}e^{-Z_{t-1,A-1}} + N_{t-1,A}e^{-Z_{t-1,A}}$$

Total mortality is $Z_{t,a} = F_t s_a^{C_k} + M_t^i + M_t^p s_a^p$, $a = 1,\ldots,4$, for immature cod and $Z_{t,a} = F_t s_a^{C_k} + M_t^m + M_t^p s_a^p$, $a = 5,\ldots,A$ for mature cod.

Expected numbers of catch at age follow the Baranov catch equation (Quinn and Deriso 1999): $C_{t,a} = N_{t,a} \dfrac{F_t s_a^{C_k}}{Z_{t,a}}(1 - e^{-Z_{t,a}})$.

Because of a change in research-vessel trawl gear in 1982 from Yankee 36 with width × vertical headline 11.0×3.4 m^2 to Western IIA with 12.5×4.6 m^2, survey catchability (q) was assumed to be different for the two periods. Thus, the expected numbers at age a for research surveys were calculated as $N_{t,a}^s = q_j N_{t,a} s_a^s$, where $j = 1$ for the period 1970–1981 and $j = 2$ for 1982–1997. Catchabilities q_1 and q_2 were arbitrarily set at 0.4 and 0.6, resepectively, the ratio of which is approximately the difference in net openings. Other levels were tried for evaluating sensitivity to their changes. Expected numbers of consumption at age a by grey seals in year t is

$$C_{t,a}^p = N_{t,a} \frac{M_t^p s_a^p}{Z_{t,a}}(1 - e^{-Z_{t,a}})$$

Parameters estimated include the time-dependent deviation terms η_t^R, η_t^F, η_t^p, η_t^i, and η^m. In addition, the following selectivity parameters for research survey, commercial fishing, and predation

Fig. 2. Parameter estimates obtained using consumption data of constant cod fraction in seal diet under three assumptions of catchability (q): q_1 (before 1982) and q_2 (1982 and afterwards) are set at 0.4 and 0.6 (line without symbols), both at 0.3 (line with solid squares), and 0.8 (line with solid triangles), respectively. The estimates include predation mortality averaged over ages 1–4, M^p (a), natural mortality of immature cod, M^i (b), natural mortality of mature cod, M^m (c), instantaneous fishing mortality of fully recruited fish, F (d), recruitment, R (e), and spawning-stock biomass, SSB (f).


were estimated: γ^s, δ^s, γ^{C_k}, δ^{C_k}, s_1^p, γ^p, and δ^p. Parameter estimation was accomplished using the software AD Model Builder, which estimates parameters in a step-by-step fashion known as a multiphase procedure (Otter Research Ltd. 1998). A nonlinear least-squares (NLS) parameter-estimation procedure was applied. The NLS is robust to error structure in the data, such as in multinomial catch-at-age data, and could be expected to find parameter estimates more rapidly than the multinomial maximum likelihood method (Kimura 1990). Square-root transformation following Quinn et al. (1998) was used for all data. A logarithmic transformation was also applied and yielded quantitatively similar results, which are not presented. The following objective function is minimized for estimating parameters:

$$f = \lambda_C \sum_t \sum_a \left(\sqrt{\widetilde{C}_{t,a}} - \sqrt{C_{t,a}} \right)^2$$

$$+ \lambda_{N^s} \sum_t \sum_a \left(\sqrt{\widetilde{N}_{t,a}} - \sqrt{N_{t,a}^s} \right)^2$$

$$+ \lambda_{C^p} \sum_t \sum_a \left(\sqrt{\widetilde{C}_{t,a}^p} - \sqrt{C_{t,a}^p} \right)^2$$

$$+ \lambda_{M^i} \sum_t (\eta_t^{M^i})^2 + \lambda_{M^m} \sum_t (\eta_t^{M^m})^2$$

Weighting factors λ_C, λ_{N^s}, and λ_{C^p} were determined on the basis of the inverse of their residual variances and were set at 1.0, 0.3, and 1.0, respectively. In trials, parameter estimation was little affected by weighting factors of different data sources, which is consistent with the conclusion in Fu (2000). The terms $\lambda_{M^i} \sum_t (\eta_t^{M^i})^2$ and $\lambda_{M^m} \sum_t (\eta_t^{M^m})^2$ are penalties controlling the degree of variability in the time series of M^i and M^m estimates from year to year. The values of λ_{M^i} and λ_{M^m} are calculated as the product of $\widetilde{N}_{t,a}$ residual variance, λ_{N^s}, an assumed coefficient of variation of $\widetilde{N}_{t,a}$ (Fu and Quinn 2000), and the relative variation of M^i and M^m. We assigned 7500.0 and 5000.0 to λ_{M^i} and λ_{M^m}, respectively. The sensitivity of parameter estimation to the choice of λ_{M^i} and λ_{M^m} levels was examined.

Standard error and retrospective analysis

The bootstrap method (Efron and Tibshirani 1993) was used to estimate standard errors for the parameter estimates and predicted spawning stock biomass (SSB). Residuals from the original model were resampled. Parameter estimation was repeated 500 times using bootstrap data. Retrospective analysis (Mohn 1999) was conducted to evaluate the ability of the model to estimate parameters for the terminal years. This was done by reestimating parameters after leaving out successive terminal data with the full series, 1970–1997, which was eventually reduced to 1970–1983.
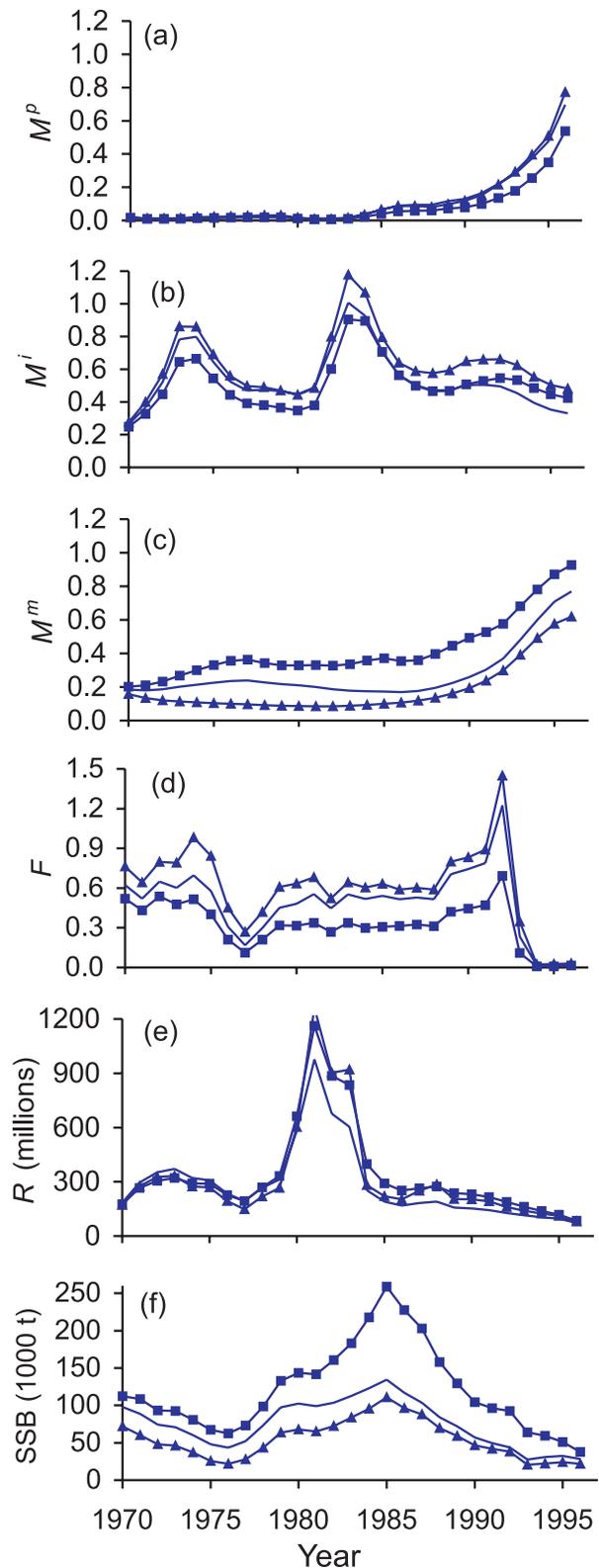
Results

Sensitivity to catchability

Survey data, $\widetilde{N}_{t,a}$, are calibrated to the estimated population number at age using the catchability from research sur-

veys. Fu (2000) demonstrates that q cannot be estimated with sufficient accuracy simultaneously with natural mortality (M), and it is better to keep q at a given level while estimating M each year even when there is variation in q (Fu and Quinn 2000). To examine how q affects the estimation of population parameters, we adopted various time-invariant levels of q and compared the parameter estimates and residual sum of squares (RSS). For purposes of the sensitivity evaluation, a constant fraction of cod in the seal diet is assumed to eliminate the nuisance effect of different $\tilde{C}_{t,a}^p$ values corresponding to different levels of q. In addition to the initially set q_1 and q_2 values of 0.4 and 0.6, alternative levels of 0.3 and 0.8 are also tried.

The estimation of M^p (shown as the average over ages 1–4), M^i, and R is robust to the assumed levels of q (Fig. 2). However, the estimated M^m, F, and SSB change dramatically in magnitude, with M^m and SSB decreasing and F increasing, when q increases from 0.3 to 0.8. The parameter estimates with q_1 and q_2 values of 0.4 and 0.6 are in between, and RSS is the lowest (Table 1a). The sensitivity evaluation suggests that the assumption concerning q is reasonable and will not affect the overall conclusions that we will draw hereinafter.

Sensitivity to consumption data

Because the estimated number at age consumed by grey seals, $\tilde{C}_{t,a}^p$, depends on the assumption made regarding cod fraction in the seal diet, it is necessary to explore predation scenarios (constant- and proportional-fraction sets of $\tilde{C}_{t,a}^p$) and examine how they affect the estimation of other parameters. In addition, we also estimate parameters after excluding the seal-consumption data to evaluate the performance of partition of M.

The estimates of M^m, F, and SSB are nearly identical under the three scenarios of seal consumption: (1) assuming a constant fraction, (2) assuming a proportional fraction, and (3) excluding the consumption data (Fig. 3). Assuming a constant fraction results in higher estimates of M^i (except for the last 2 years) and R. The R estimates from the third scenario (with consumption data excluded) are closer to those from the second scenario, which assumes a proportional fraction. Before 1983, when M^p was small, the M^i estimates from the third scenario are also closer to those from the second scenario. When the consumption data are excluded, the estimate of M^i rises gradually after 1988, reflecting the increase in M^p. The RSS from the second scenario (proportional fraction) is the lowest, and it increases drastically when the consumption data are excluded (Table 1b). In the following analyses, the data $\tilde{C}_{t,a}^p$ from the second scenario are used.

Sensitivity to penalty weighting

The estimates of M^i and M^m are closely related to the weighting factors λ_{M^i} and λ_{M^m} with higher levels resulting in reduced variations. Simulation studies indicate that appropriate weighting levels are related to measurement error in research-survey data (Fu 2000). We increased λ_{M^i} and λ_{M^m} by a factor of 3 from the originally assigned levels and then reduced them by factors of 3 and 6 to check sensitivity.

When the levels of λ_{M^i} and λ_{M^m} increase threefold, the estimates of M^i and M^m are nearly flat (Fig. 4). Recruitment

Fig. 3. Parameter estimates obtained using consumption data of constant fraction in seal diet (line with solid squares) and proportional fraction (line without symbols) and obtained with consumption data excluded (line with solid triangles). For details see Fig. 2.
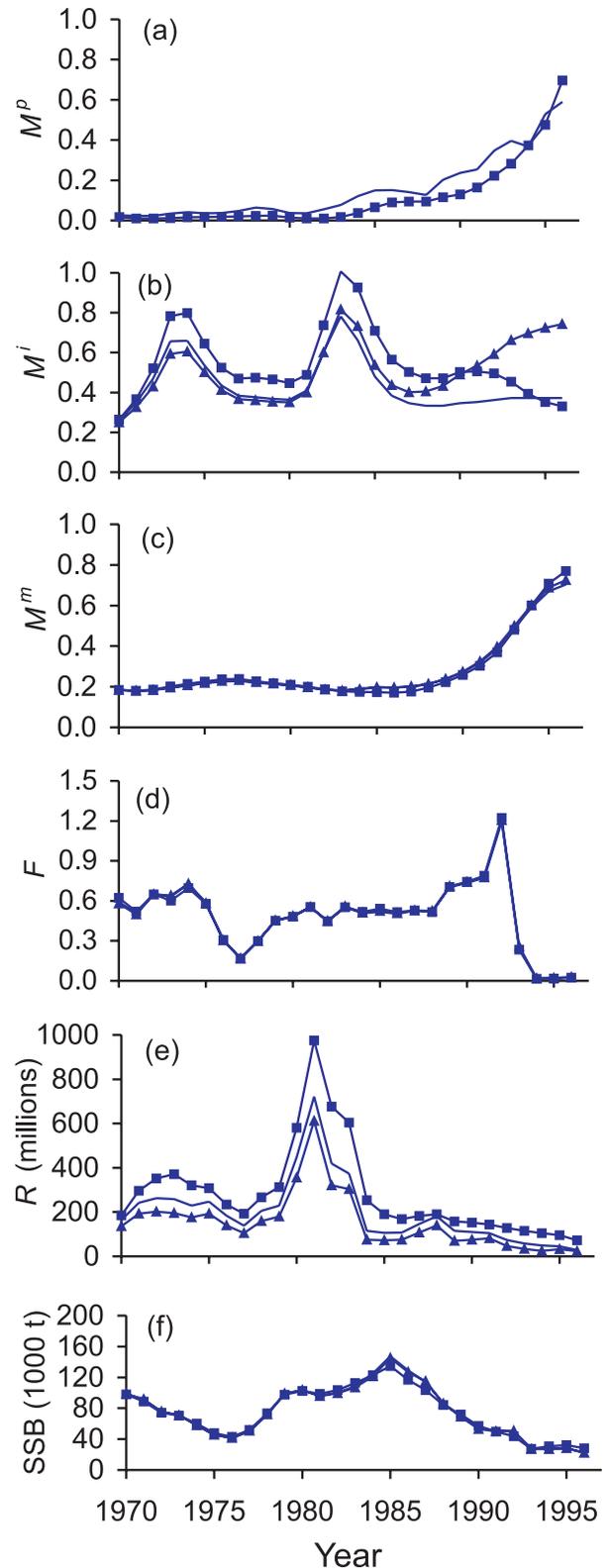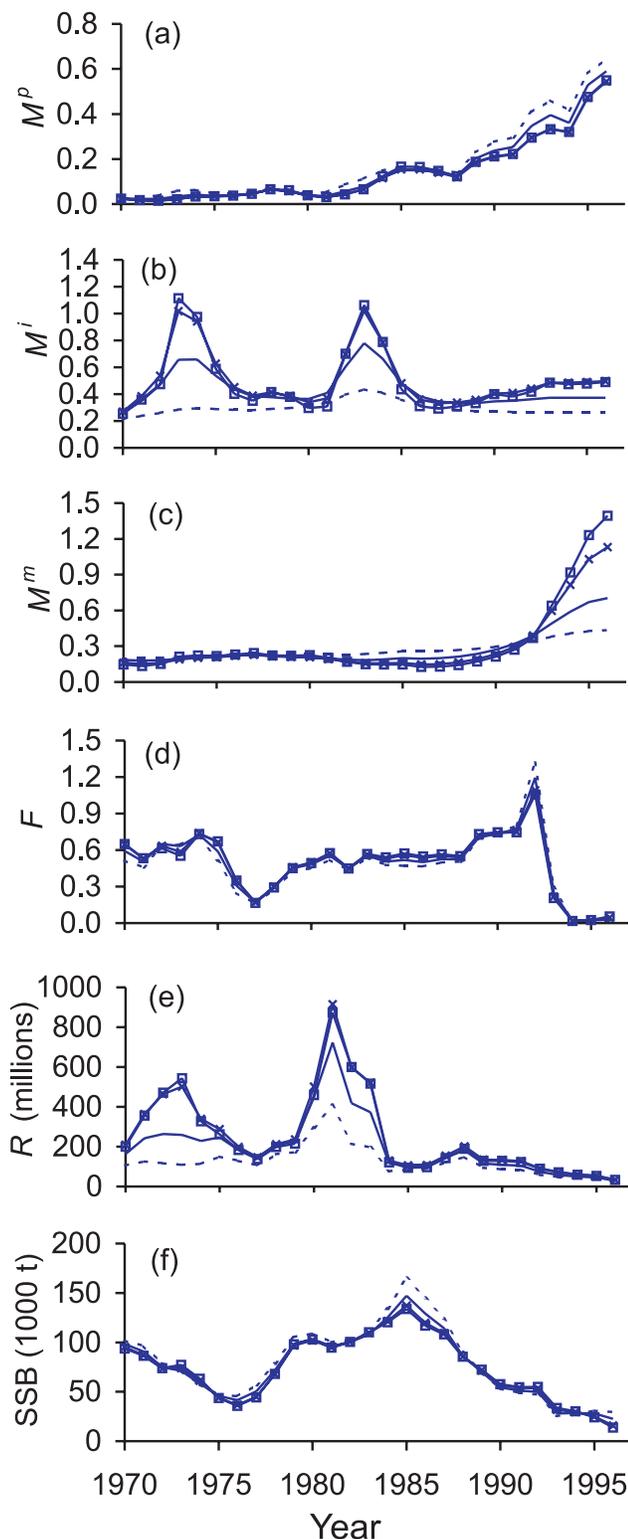
1618

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

Fig. 4. Parameter estimates obtained using four sets of penalty weighting factors λ_{M^i} and λ_{M^m}: 7500 and 5000 (line without symbols), 3 times larger (broken line), 3 times smaller (line with ×), and 6 times smaller (line with open squares). For details see Fig. 2.

Table 1. Residual sums of squares (RSS) from scenarios of sensitivity evaluation on catchability (*a*), seal consumption (*b*), and penalty weightings of natural mortality variability, λ_{M^i} and λ_{M^m} (*c*).

Catchability	Seal consumption	λ_{M^i} and λ_{M^m}	RSS
(*a*) **Catchability**			
0.3	Constant	7500, 5000	165 923
0.8	Constant	7500, 5000	188 198
0.4, 0.6	Constant	7500, 5000	162 467
(*b*) **Seal consumption**			
0.4, 0.6	Constant	7500, 5000	162 467
0.4, 0.6	Fraction	7500, 5000	157 010
0.4, 0.6	Excluded	7500, 5000	258 470
(*c*) **Penalty weightings of natural mortality variability,** λ_{M^i} **and** λ_{M^m}			
0.4, 0.6	Fraction	7500, 5000	162 467
0.4, 0.6	Fraction	2500, 1600	137 419
0.4, 0.6	Fraction	1250, 830	130 773
0.4, 0.6	Fraction	22500, 15000	185 962

M^i, M^m, and R; however, the overall time trend in the parameter estimates is not changed. Reducing λ_{M^i} and λ_{M^m} by a factor of 6 results in similar estimates of M^i and R, but much higher M^m, in the last 4 years. The RSS declines when the weighting factors are reduced (Table 1*c*), Although lower levels of the weighting factors are desired under low measurement errors with a resultant better fit to the data (Fu 2000), the uncertainty in the accuracy of the survey data led us to retain the intermediate levels.
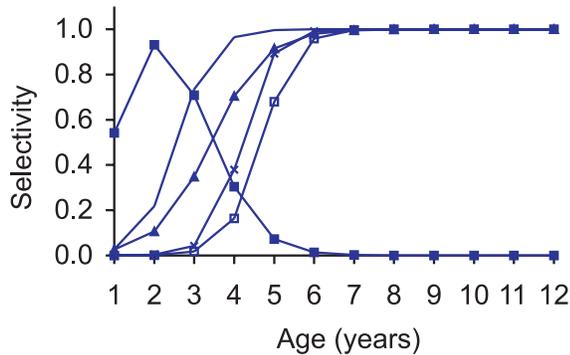
Parameter estimation and standard error

Using catchability q_1 and q_2 of 0.4 and 0.6, respectively, the consumption scenario of proportional fraction, and the originally assigned penalty weighting factors for natural mortality deviations, we estimated the population parameters. Figure 5 shows the selectivity curves. Standard errors of the mortality parameters, R, and SSB were obtained from the bootstrap procedure (Fig. 6). The estimated M^p averaged over ages 1–4 has increased dramatically since 1988, and is nearly twice as large as M^i in the terminal year. The estimated M^i has two peaks, one in the early 1970s and another in the early 1980s, but has remained at a stable level since the mid-1980s. In contrast, the estimated M^m remains around 0.2 until 1990, after which it increases dramatically. The estimated F is around 0.7 in the 1970s, declines to 0.17 in 1977 at the time of extension of jurisdiction, and remains around 0.5 throughout the 1980s. Fishing mortality starts to climb in 1989 and peaks at 1.2 in 1992 before the fishery closure took place in 1993. The estimated R has one prominent peak in the early 1980s, and declines steadily after 1988. The estimated SSB declines steadily in the 1970s before starting to climb in 1977. SSB peaks in 1985, but declines steadily afterwards. Estimated total mortality from the model for both immature and mature cod agrees well, in general, with that directly calculated from the survey data (Fig. 7). However, survey data give much higher estimates of M^m for the last 3 years.

Retrospective analysis

Compared with previous results based on SPA (Mohn et al. 1998), retrospective analysis produces a much less severe

estimates decrease correspondingly and the RSS increases substantially. When the levels of λ_{M^i} and λ_{M^m} are reduced by a factor of 3, there are more dynamics in the estimates of

Fig. 5. Selectivity curves for predation (line with solid squares), survey gear (line without symbols), and commercial gear from 1970 to 1976 (line with solid triangles), from 1977 to 1982 (line with ×), and from 1983 to 1997 (line with open squares).

Fig. 6. Parameter estimates obtained using catchability q_1 and q_2 of 0.4 and 0.6, consumption data of proportional fraction in seal diet, and penalty weighting factors λ_{M^i} and λ_{M^m} of 7500 and 5000. For details see Fig. 2. Standard errors are shown as bar lines.

retrospective pattern in the estimates of all parameters except M^m (Fig. 8). The shape of the M^m estimates in the 1990s changes dramatically, from increasing to leveling out, when the last 2 years' data are removed. In addition, the estimates of M^i and R with data only up to 1984 deviate substantially from the values obtained from the analysis of the entire historical data series.

Discussion

This paper presents an age-structured model that uses multiple data sources from commercial-fishery, research-survey, and seal-diet analysis. This is the first stock-assessment study that estimates annual variations in natural mortality of both immature and mature cod. Our estimates of mortality indicate that except for the increase in F from 0.78 in 1991 to 1.2 in 1992, there is no dramatic increase in M^p, M^i, and M^m over the years 1991 and 1992. Our major conclusion is that the abrupt decline of the 4VsW cod stock in the early 1990s is unlikely to have been due to a sudden increase in M, and fishing appears to have been the primary cause.

The estimation of natural mortality indicates that M^i is more variable than M^m, which remains around 0.2 except in the last 4 years. Simulation studies indicate that M should be estimated annually when it varies over time (Fu and Quinn 2000). The variability in the M^i estimates suggests that M^i should be estimated each year as has been done here. When consumption data are excluded from the parameter-estimation procedure, the estimated M^i increases continuously after 1988, consistent with the increasing trend in the M^p estimates. This further suggests that estimating M^i annually is important, particularly when consumption data are unavailable. Estimating annual M^i captures mortality changes, whether they are due to predation or to other factors. Another major conclusion from this study is that estimates of M^p have increased dramatically since 1988 irrespective of the predation scenario. The consistency between the increasing trend in M^p and the difference between two series of M^i estimated with and without the consumption data indicates that partition of immature cod mortality into M^p and M^i is practical.
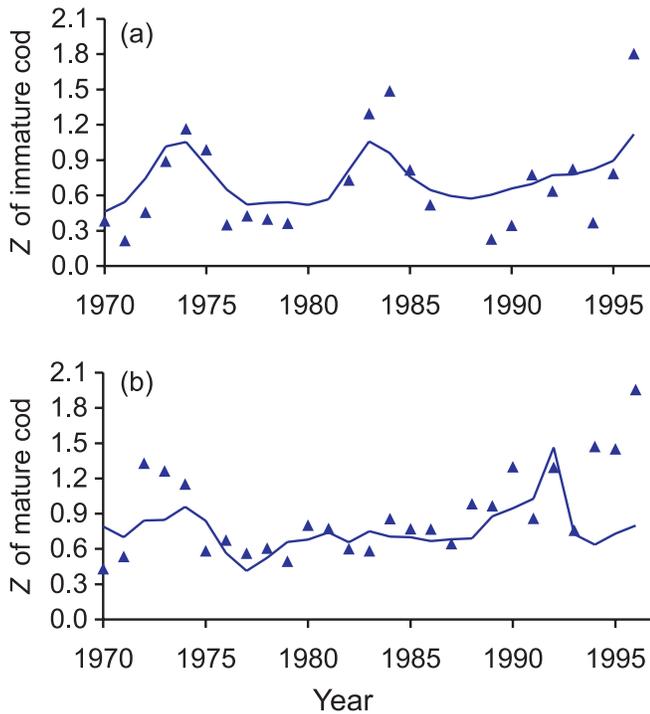
Sensitivity examination indicates that the estimate of M^i is robust to the assumption of q and primarily controlled by the
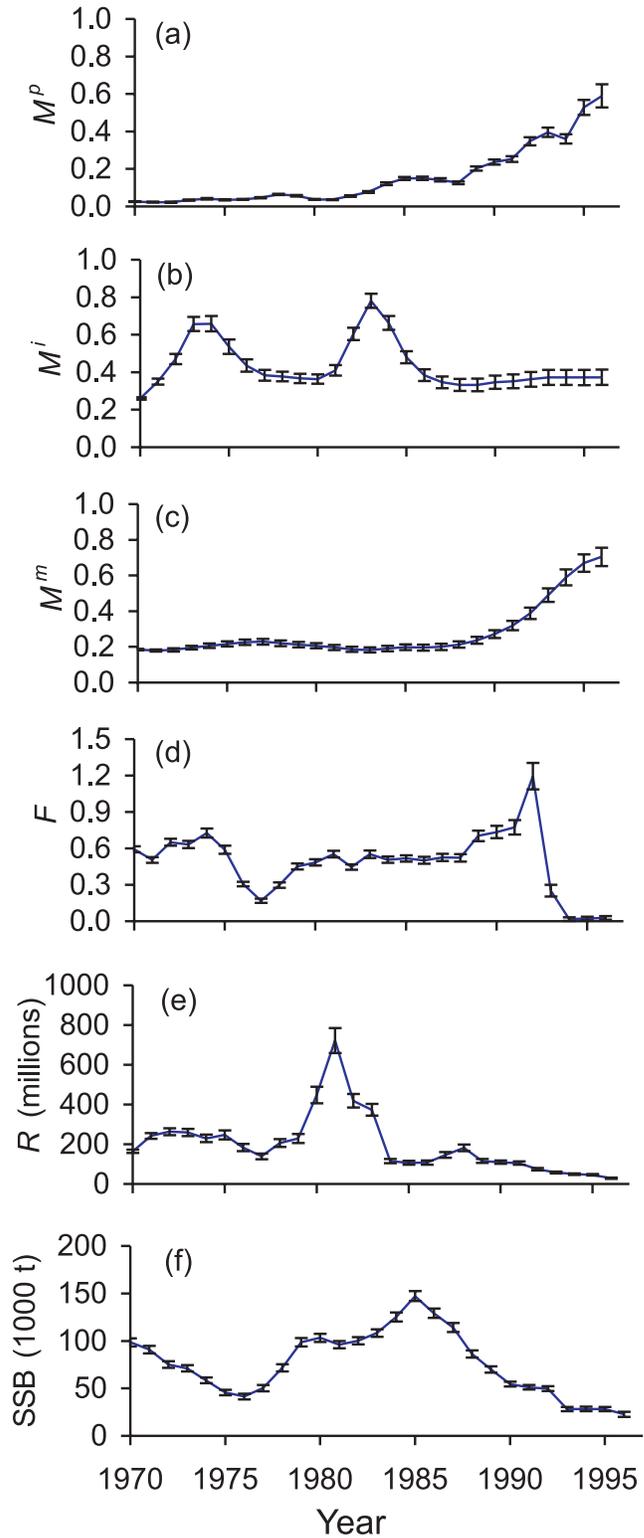
weighting factor λ_{M^i}. Smaller measurement errors in survey data favor smaller weighting. However, if measurement er-

Fig. 7. Total mortality (Z) estimated from the model (line) and solely from the survey data (solid triangles) for both immature cod (*a*) and mature cod (*b*).

Fig. 8. Parameter estimates from retrospective analyses using data from 1970 to 1983 and all the way up to 1997. For details see Fig. 2.

rors are large and a small value is assigned to λ_{M^i}, then the M^i estimates can be overly sensitive to the errors in the survey data. On the other hand, if the measurement errors are lower than assumed, we run the risk of underestimating the magnitude and variability of M^i for the three periods of peaks in M^i: the early 1970s, early 1980s, and 1990s. Nevertheless, such an underestimation would not change our view of the stock status or our conclusions.

In contrast, the estimate of M^m is closely related to the q value. The higher q value, the lower the M^m estimates will be. Nevertheless, the time trend is not changed if the assumption of the overall q level is wrong. The estimates of M^m are rather stable before the decline of the stock in 1990s; however, they have increased by a factor of 3 over the last 7 years. It was noted that M^m was the only variable that displayed a severe retrospective pattern. Removing the last 2 years' data changes the shape of the M^m estimates completely. Further examination of the trend towards an increase in M^m estimates indicates that it is primarily caused by the low survey values of $\tilde{N}_{t,a}$ in 1996 and 1997. Replacing these 2 years' data by those from 1995 gives a much slower increase in the M^m estimates.

Why did the survey estimates of mature cod abundance in 1996 and 1997 drop abruptly? The exact reasons are not known, but there are at least three possibilities. The first possibility is that the fish moved away and were unavailable to survey gear, as suggested by Rose et al. (2000) for the cod stocks off Newfoundland. However, this possibility is slim for the 4VsW cod stock because there is no evidence that cod abundance increased in other adjacent areas. The second possibility is that mature cod simply died, as the high M^m estimates suggest. Fishermen videotaped numerous carcasses
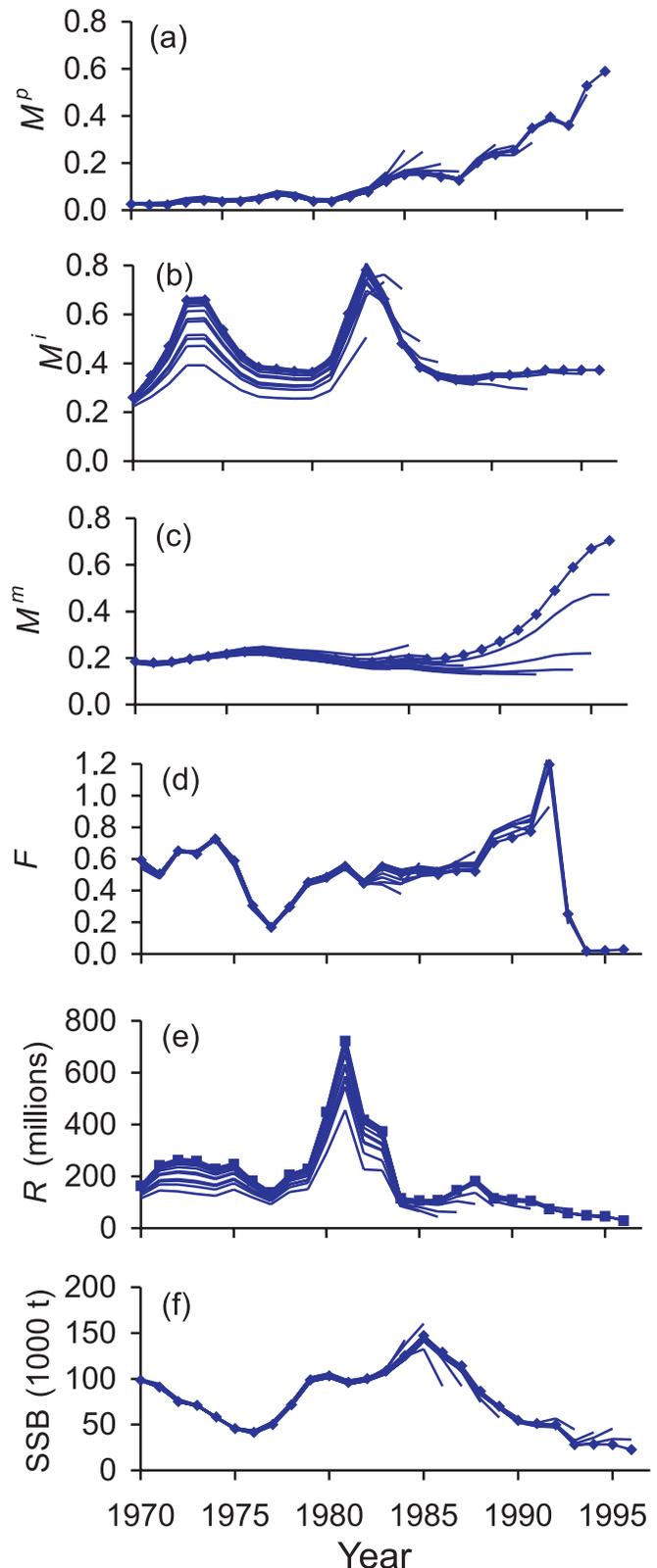
Fig. 9. (*a*) Comparisons among portions of immature cod biomass lost as a result of fishing mortality (grey-shaded area), predation mortality (open area), average immature-cod mortality, M^i (or M^i if it is less than the average) (dotted area), and the portion of M^i beyond its average (hatched area). The area below the broken line represents immature cod biomass that survived each year. (*b*) Comparisons among portions of mature cod biomass lost as a result of fishing mortality, predation mortality, 0.2 (or M^m if it is less than 0.2), and the portion of M^m beyond 0.2. The area below the lower broken line represents the mature cod biomass that survived each year, and that below the higher broken line represents the biomass of age 4 cod that survived each year. In *c* and *d*, biomass loss is shown as a percent for immature and mature cod, respectively.
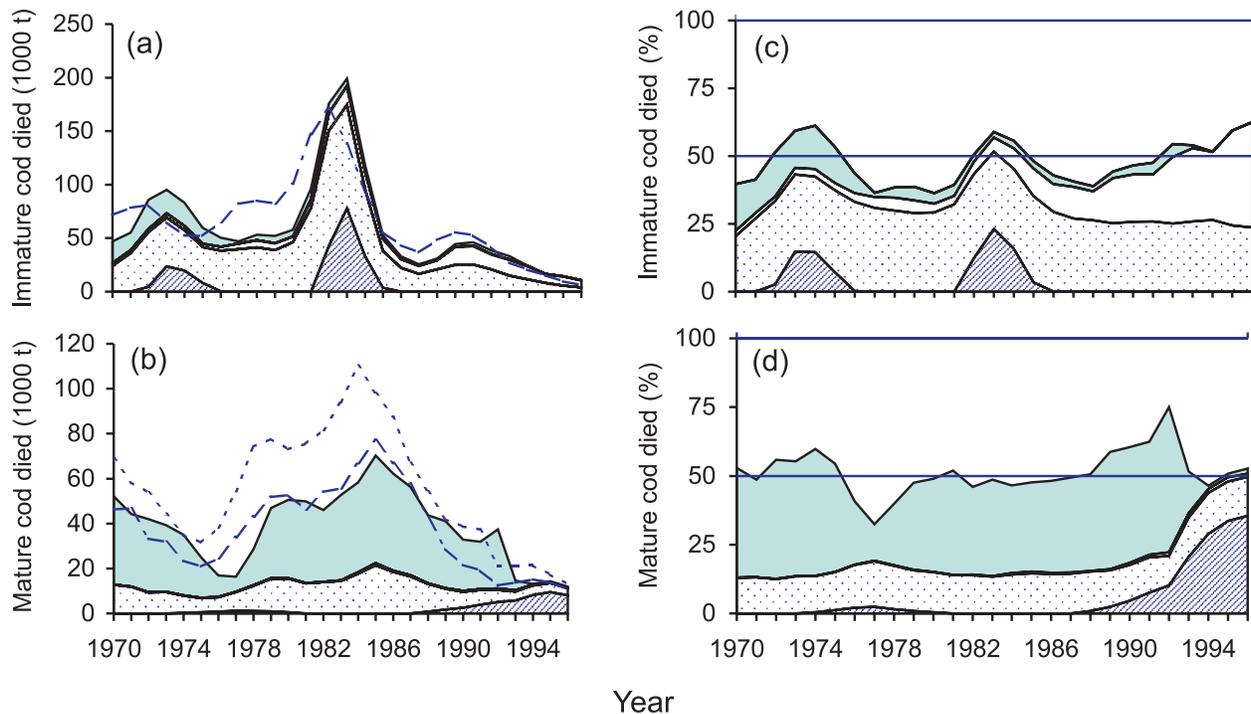
of large cod left by seals that fed solely on the belly of these fish off Newfoundland, a form of predation not detectable by diet-estimation studies. The third possibility is that low recruitment throughout the early 1990s failed to replenish the mature cod stock. The low recruitment may have been due to environmental changes that reduced reproductive potential (Lambert and Dutil 2000); environmental changes are evident from the changes in species composition (Frank et al. 1996) and physical oceanography (Drinkwater and Mountain 1997). If the last two possible scenarios did occur, failure of the 4VsW cod stock to recover after the moratorium on commercial fishing would be expected.

Overall, the significant advance in our work is the relaxation of the assumption of a constant M, an assumption that can be easily violated (Fu 2000; Shelton and Lilly 2000). The estimation of annual variations in M leads to changes in the R estimates. Our R estimates are generally larger than those in Mohn et al. 1998, particularly for the early 1980s. Natural mortality and recruitment are positively correlated. When high M and high R values coexist, assessment models that assume a low constant M, such as 0.2, would underestimate the corresponding R. Thus, Mohn et al. (1998) appear to have systematically underestimated R. The extremely high R estimates from our model for the early 1980s are consistent with the research surveys that also reveal an extremely high R value in the early 1980s (Mohn et al. 1998). Overall, R estimates from assessment models of constant M could largely deviate from the true values if M, in fact, varies over

time. Estimating annual variations in M is essential to a better understanding of the underlying population dynamics.

After the cod stocks off southern Labrador and eastern Newfoundland collapsed suddenly in 1992, it was hypothesized that M increased in 1991 (Myers and Cadigan 1995). A precipitate loss of 700 million fish was estimated for cod older than age 2 in 1991, corresponding to an average M value of 1.14 compared with the level of 0.2 assumed in cod-stock assessments (Shelton and Lilly 2000). However, the hypothesis of a sudden increase in M in 1991 was rejected (Hutchings and Myers 1994; Myers and Cadigan 1995), and fishing mortality was regarded as sufficient cause for the collapse of the stock (Myers et al. 1996; Walters and Maguire 1996). Our estimates of mortalities F, M^p, M^i, and M^m before 1993 support the finding in Myers and Cadigan (1995). In particular, when the data up to 1995 are used (leaving out the data from 1996 and 1997), the estimated M^m in the early 1990s declines slightly.

Could a precipitate drop in cod biomass similar to that of the cod stocks off southern Labrador and eastern Newfoundland (Shelton and Lilly 2000) also have happened to the 4VsW cod stock? We take advantage of the estimates of annual variations in mortality and recruitment to explore population dynamics through the entire observation history. To reveal biomass loss due to various mortalities, we partitioned the total biomass loss of mature cod into four parts: loss due to F, M^p, 0.2 (or M^m if it is less than 0.2), and the portion of M^m beyond 0.2. Although the cod fishery in 4VsW appears

to have collapsed over 1991 and 1992, the decline in survival of mature cod has taken place since 1985 (Fig. 9). Since 1988, the quantity of fish that died has been greater than that which survived. In 1992, the percent of mature cod that died reached a peak. Replenishment from age 4 cod has been low since 1985, except for the increases in 1990 and 1991, corresponding to the relatively high R estimates in 1987 and 1988. However, the abundance of surviving age 4 cod dropped dramatically in 1992 despite the fact that M^i and M^m remained at historically low levels. Off southern Labrador and eastern Newfoundland, young cod aged 4 and 5 in 1990 and 1991 resulting from high recruits in 1986 and 1987 were similarly predominant in the catches made just before the fishery closure, which was attributed to the relative absence of older fish (Myers et al. 1996). With M^m remaining around the historical average level of 0.2, it can be concluded that a high F value and insufficient recruitment of age 4 cod to the mature cod stock have contributed to the continuous decline in mature cod biomass.

To envisage the biomass dynamics of immature cod, we also partitioned the total biomass loss into four parts: loss due to F, M^p, average of the M^i estimates (or M^i if it is below the average), and the portion of M^i beyond its average. Before the fishery collapse, there were two periods when loss of immature cod biomass exceeded 50%, one in the early 1970s and another in the early 1980s. The large loss of immature cod biomass in the early 1980s may have contributed to the reduction in recruitment of age 4 cod to the mature cod stock. The causes of the large biomass loss are unknown, but it is consistent with the widely discussed period of extensive discarding of undersized fish (Mohn et al. 1998). Overall, we conclude that fishing mortality may have been the primary cause of the collapse of the 4VsW cod stock.

It was suggested that the unbridled increase in F just before the collapse was caused by overestimation of stock size (Walters and Maguire 1996), statistical bias inherent in the estimation procedures (Myers et al. 1996), or increased concentration of cod at low stock size (Hutchings and Myers 1994; Hutchings 1996; Rose et al. 2000). Based on their statistical analysis, Myers et al. (1995) suggested that the cod stocks would recover after the moratorium on fishing. However, this has not happened up to this point, 10 years after the moratorium. Why are the stocks not recovering? What happened to the cod stocks after the collapse? Our M^p, M^i, and M^m estimates for the 4VsW cod stock after its collapse demonstrate that M^p became an important factor affecting the survival of immature cod in the 1990s. Throughout the 1990s, the proportion of immature cod that died was greater than that which survived. Mature cod may also have been subject to high natural mortality since the mid-1990s. Recruitment was low in the 1990s. These three factors have contributed to the failure of the stock to recover.

Acknowledgements

References

deYoung B., and Rose, G.A. 1993. On recruitment distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

Drinkwater, K.F., and Mountain, D.G. 1997. Climate and oceanography. *In* Northwest Atlantic groundfish: perspectives on a fishery collapse. *Edited by* J. Boreman, B.S. Nakashima, J.A. Wilson, and R.L. Kendall. American Fisheries Society, Bethesda, Md. pp. 3–25.

Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **57**: 826–836.

Dutil, J.-D., Castonguary, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **56**: 1818–1831.

Efron, B., and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall, New York.

Fanning, L.P., Mohn, R.K., and MacEachern, W.J. 1996. Assessment of 4VsW cod in 1995 with consideration of ecological indicators of stock status. DFO Atlantic Fisheries Rec. Doc. 96/27.

Frank, K.T., Carscadden, J.E., and Simon, J.E. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can. J. Fish. Aquat. Sci. **53**: 1473–1486.

Fu, C. 2000. Length-based models and population analyses for northern shrimp *Pandalus borealis* Krøyer. Ph.D. thesis, University of Alaska Fairbanks, Juneau.

Fu, C., and Quinn, T.J., II. 2000. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* Krøyer in Kachemak Bay, Alaska. Can. J. Fish. Aquat. Sci. **57**: 2420–2432.

Halliday, R.G. 1975. Eastern Scotian Shelf cod: a reconstruction of possible events in the fishery in 1958 to 1974 and a re-estimation of potential yield. ICNAF Res. Doc. 75/IX/136.

Halliday, R.G., and Pinhorn, A.T. 1990. The delimitation of fishing areas in the northwest Atlantic. J. Northw. Atl. Fish. Sci. **10**: 1–51.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Kimura, D.K. 1990. Approaches to age-structured separable sequential population analysis. Can. J. Fish. Aquat. Sci. **47**: 2364–2374.

Lambert, Y., and Dutil, J.-D. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Can. J. Fish. Aquat. Sci. **54**: 2388–2400.

Lambert Y., and Dutil, J.-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Can. J. Fish. Aquat. Sci. **57**: 815–825.

Mohn, R.K. 1999. The retrospective problem in sequential population analysis: an investigation using cod fishery and simulated data. ICES J. Mar. Sci. **56**: 473–488.

Mohn, R.K., and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Can. J. Fish. Aquat. Sci. **53**: 2722–2738.

Mohn, R.K., Fanning, L.P., and MacEachern, W.J. 1998. Assessment of 4VsW cod in 1997 incorporating additional sources of mortality. Canadian Stock Assessment Secretariat Res. Doc. 98/78.

Myers, R.A., and Cadigan, N.G. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. **52**: 1274–1285.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science (Washington, D.C.), **269**: 1106–1108.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1996. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. **138**: 293–308.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol. Appl. **7**: 91–106.

Otter Research Ltd. 1998. An introduction to AD Model Builder for use in nonlinear modeling and statistics. Otter Research Ltd., Nanaimo, B.C.

Quinn T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Quinn, T.J., II, Turnbull, C.T., and Fu, C. 1998. A length-based population model for hard-to-age invertebrate populations. *In* Fishery stock assessment models. *Edited by* F. Funk, T.J. Quinn II, J. Heifetz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and C.-I. Zhang. Sea Grant Rep. 98-01, University of Alaska, Fairbanks. pp. 531–556.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**(Suppl. 1): 118–127.

Rose, G.A., deYoung, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Can. J. Fish. Aquat. Sci. **57**: 644–663.

Shelton, P.A., and Lilly, G.R. 2000. Interpreting the collapse of the northern cod stock from survey and catch data. Can. J. Fish. Aquat. Sci. **57**: 2230–2239.

Walters, C., and Maguire, J.-J. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. **6**: 125–137.