Estimation of the parameters of fish stock dynamics from catch-at-age data and indices of abundance: can natural and fishing mortality be separated?

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Abstract: Models for fluctuations in size of fish stocks must include parameters that describe expected dynamics, as well as stochastic influences. In addition, reliable population projections also require assessments about the uncertainties in estimates of vital parameters. Here we develop an age-structured model of population dynamics based on catch-at-age data and indices of abundance in which the natural and fishing mortality are separated in a Bayesian state–space model. Markov chain Monte Carlo methods are used to fit the model to the data. The model is fitted to a data set of 19 years for Northeast Arctic cod (*Gadus morhua*). By simulations of the fitted model we show that the model captures the dynamical pattern of natural mortality adequately, whereas the absolute size of natural mortality is difficult to estimate. Access to long time series of high-quality data are necessary for obtaining precise estimates of all the parameters in the model, but some parameters cannot be estimated without including some prior information. Nevertheless, our model demonstrates that temporal variability in natural mortality strongly affects perceived variability in stock sizes. Thus, using estimation procedures that neglect temporal fluctuations in natural mortality may therefore give biased estimates of fluctuations in fish stock sizes.

Résumé : Les modèles fluctuation de la taille des stocks de poissons doivent inclure des paramètres qui décrivent la dynamique attendue ainsi que les influences stochastiques. De plus, des projections fiables de la population nécessitent une évaluation des incertitudes dans les estimations des paramètres vitaux. Nous mettons au point un modèle de la dynamique de la population structuré en fonction de l'âge qui est basé sur les données de captures en fonction de l'âge et les indices d'abondance dans lequel la mortalité naturelle et la mortalité due à la pêche sont séparées dans un modèle état–espace bayésien. Des méthodes de Monte Carlo par chaîne de Markov servent à ajuster le modèle aux données. Nous ajustons le modèle à une matrice de données récoltées sur 19 années chez la morue (*Gadus morhua*) du nord-est de l'Arctique. Par simulations du modèle ajusté, nous montrons que le modèle capture adéquatement le patron dynamique de la mortalité naturelle, bien que la taille absolue de la mortalité naturelle soit difficile à estimer. Il est nécessaire d'avoir accès à de longues séries chronologiques de données de haute qualité pour obtenir des estimations précises de tous les paramètres du modèle, mais certains paramètres ne peuvent être estimés sans l'inclusion de renseignements a priori. Néanmoins, notre modèle démontre que la variabilité temporelle de la mortalité naturelle affecte fortement la variabilité perçue des tailles des stocks. Ainsi, l'utilisation de procédures qui négligent les fluctuations temporelles de la mortalité naturelle peut donner des estimations erronées des fluctuations dans les tailles des stocks de poissons.

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Introduction

A sustainable management strategy of commercial fish stocks is dependent on understanding how harvesting may influence future stock sizes. This requires that we are able to estimate parameters such as density and causes of mortality with sufficient precision. Accordingly, we must also estimate the stochastic influences on the population dynamics, in most cases arising from stochastic variation in the environment (Lande et al. 2003). It is important to separate the environmental noise from the stochasticity that is caused by uncertainties in parameter estimates and errors in estimates of stock size (Freckleton et al. 2006). Developing population models of some credibility requires that both types of sto-

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chastic influences are properly assessed when making predictions that form the basis for management decisions (Walters and Martell 2004).

Catch-at-age data probably represent the most important data source for assessment of fish stock size (see reviews in, e.g., Megrey (1989), Quinn and Deriso (1999), and Millar and Meyer (2000)). Recent analyses of catch-at-age data have been refined to consider process and measurement errors using traditional frequentist techniques (e.g., Gudmundsson 1994; Schnute and Richards 1995; Richards and Schnute 1998), as well as Bayesian methods (e.g., Schnute 1994; Punt and Hilborn 1997; Millar and Meyer 2000). Information about the precision in the data is necessary for obtaining unbiased estimates of population parameters (de Valpine and Hastings 2002; Dennis et al. 2006; and Freckleton et al. 2006, and references therein). Furthermore, whatever the statistical approach used, separating natural fluctuations in mortality from mortality due to fishing is crucial for obtaining reliable estimates of stock size and detecting changes in harvest rates (Walters and Martell 2004).

It is commonly assumed that natural mortality of adults is known and constant (e.g., Hilborn and Walters 1992; Quinn and Deriso 1999; International Council for the Exploration of the Sea (ICES) 2005). Even if wrong values of natural mortality are chosen and if fluctuations in total mortality are dominated by fishing mortality, estimates of stock size, although potentially seriously biased, may still capture the temporal dynamics in the stock. Methods for estimating natural mortality based on capture–recapture analyses of tagged individuals (Seber 1982; Quinn and Deriso 1999) are often of limited use for marine fish populations because of high costs involved in the necessary sampling (e.g., tagging of fish). Most of the applied methods are based on samples of stomach contents and estimation of additional mortality by predation of other species in a multispecies context (ICES 2005) or, as for the Northeast Arctic cod, by cannibalism (ICES 2004).

The stochastic processes in the population dynamics along with the uncertainty in the available data for assessing fish stocks emphasises the need of probabilistic approaches for quantifying the risks concerning status of stock and management decisions. One model class capable of addressing numerous sources of variability is the state–space framework, i.e., the available data (the estimates of catch at age and indices) are noisy observations from a hidden dynamical system (the population). For instance, Gudmundsson (1994) models the fishing mortality as a stochastic process where natural mortality is assumed known and constant, whereas Lewy and Nielsen (2003) assume that stock survival (the sum of natural and fishing mortality) for a given mortality rate is a stochastic process. The variability in fishing mortality is thus confounded with the variability in natural mortality (Lewy and Nielsen 2003). In the models of Schnute and Richards (1995) and Millar and Meyer (2000), natural mortality is considered unknown, but the stochastic variations in natural mortality are not separated from the variations in fishing mortality.

In this paper we present a model in a state–space framework. The model is age-structured, and both natural and fishing mortality are considered as stochastic processes with unknown parameters. The model takes into account that the input data are uncertain. We use a Bayesian approach and Markov chain Monte Carlo methods to fit the model to the data (see Clark 2005). Starting with a complex model, we show how model complexity must be reduced (e.g., Ludwig and Walters 1989; Richards and Schnute 1998) to obtain reliable estimates of population sizes, as well as population dynamical parameters. The model is fitted to data for Northeast Arctic cod (*Gadus morhua*) in the Barents Sea, and the fit is evaluated by simulations and compared with existing estimates for this stock.

Model

Fish stock dynamics are typically nonlinear and high-dimensional because of age structure and age-specific dynamical processes. These factors complicate traditional use of maximum likelihood for fitting state–space models to data. Linear models can be fitted using the Kalman filter and maximum likelihood when the errors are normally distributed (Schnute and Richards 1995). Methods for handling nonlinearity do exist, and Gudmundsson (1994) applied the extended Kalman filter to approximate the nonlinear likelihood function. Similarly, de Valpine and Hilborn (2005) and Dennis et al. (2006) fit nonlinear state–space models by a maximum likelihood approach, but without taking into account age structure. The Bayesian approach represents an alternative to the frequentist approach and has been applied increasingly within fisheries in the last decades (e.g., Patterson 1999; Millar and Meyer 2000; Lewy and Nielsen 2003). The Bayesian approach relies on evaluation of the posterior probability distribution $P(\Theta|\mathbf{Y})$ of the set of parameters Θ given data $\mathbf{Y}$, prior distribution $P(\Theta)$ of the parameters, and a likelihood function $P(\mathbf{Y}|\Theta)$. By applying Bayes theorem, the posterior distribution connects the prior distribution and the likelihood function through $P(\Theta|\mathbf{Y}) \propto P(\mathbf{Y}|\Theta)P(\Theta)$. For nonlinear and high-dimensional models, analytical evaluation of the posterior has been difficult. However, the last decade's development in computer power and numerical algorithms for sampling from the posterior, so-called Markov chain Monte Carlo (MCMC) methods (e.g., Gilks and Wild 1992; Tierney 1998; Gelman et al. 2004), has made the framework more tractable, e.g., nonlinearity does not offer any additional complexity as the distributions are evaluated numerically, and fitting complex and nonlinear models has become easier owing to the generality of the methods.

A stochastic age-structured model is developed that considers mortality as a stochastic process, decomposed into mortality caused by reported catches and natural mortality. It should be emphasised that the natural mortality must be interpreted with some care, because it also includes any unobserved fishery-induced mortality, e.g., possible discards and unreported catches (ICES (2004) and Zeller and Pauly (2005) and references therein). Random components describing the variability in each of the components are explicitly formulated.

Our approach is based on obtaining information of the hidden population dynamical process, described by the state model, from an observation model (for a similar approach, see Clark (2005), Clark and Bjørnstad (2004), and Sæther et al. (2007)). The observations are connected to the population

processes through models including error terms, allowing them to be uncertain. It is important to notice that this error in principle can not be interpreted as sampling error alone as it incorporates any deviation caused by misspecification of the functional relationship related to the true dynamical processes (see, for example, Lewy and Nielsen (2003) for a discussion).

The population dynamical model

The population size at age a in the beginning of year y, $N_{a,y}$, is connected to the population size of the same cohort the next year through

$$(1) \qquad N_{a+1,y+1} = N_{a,y} \exp(-Z_{a,y})$$

$$\text{for } a_{\min} \leq a \leq A, 1 \leq y \leq Y$$

where $Z_{a,y}$ is the mortality rate for age a in year y such that $\exp(-Z_{a,y})$ is the proportion of the cohort surviving from one year to the next. The minimum and maximum ages considered are $a_{\min}$ and A, respectively, and the years are indexed from 1 to Y, i.e., from the first to the last year considered. The mortality at age a in year y is the sum of mortality caused by fishing ($F_{a,y}$) and by natural causes ($M_{a,y}$), and thus $Z_{a,y} = F_{a,y} + M_{a,y}$.

We assume that the natural mortality at age a in year y is log-normally distributed with mean m_a. The variability in the natural mortality is decomposed into two factors: one component operating equally on all ages within year y to account for the temporal fluctuating environmental conditions influencing all ages (U_y) and the other operating independent of age and year to account for the remaining variability in natural mortality ($V_{a,y}$). More specifically,

$$(2) \qquad \log(M_{a,y}) = m_a + U_y + V_{a,y}$$

where the U_ys and $V_{a,y}$s are iid normally distributed with zero means and variances σ_ξ^2 and σ_M^2, respectively. This means that the covariance between the log natural mortalities at different ages is σ_ξ^2, and thus the correlation in log natural mortality between different ages within the year is

$$r_M = \sigma_\xi^2 / (\sigma_\xi^2 + \sigma_M^2)$$

The log fishing mortality at age a in year y is modelled as a separable model with random noise (Gudmundsson 1994):

$$(3) \qquad \log(F_{a,y}) = f_a + e_y + W_{a,y}$$

where the age-specific effect (f_a) is known as the log selectivity of the fishing fleet, the year-specific effect (e_y) indicates the log effort of the fishing fleet (e.g., Quinn and Deriso 1999), and the $W_{a,y}$s are iid normally distributed with zero mean and variance σ_F^2. Notice that the e_ys are parameters in the model and not known effort data from the fishing fleet. The selectivity at age is a measure of the mean relative proportion caught by the fishing fleet at age. Above a certain age, A^*, this quantity is set constant (when the fish is fully recruited into the fishery), $f_a = f_A$ for $a \geq A^*$. We notice that the separable model may not be applicable to all types of data if, e.g., gradual changes in the structure of the fishing fleet cause systematic changes in the selectivity. The effort of the fishing fleet is not likely to show abrupt changes with time, but rather slow fluctuations caused by gradual changes

in behaviour, development, and regulations of the fishing fleet. Accordingly, we model the effort as a random walk following a normal distribution, i.e.,

$$(4) \qquad e_y = e_{y-1} + T_y$$

where T_y is normally distributed with zero mean and variance σ_E^2. We fix the effort for the first year to 0 ($e_y = 0$) for identifiability (for a similar approach, see Gudmundsson 1994). If the changes in the effort employed by the fishing fleet are small from year to year, then the variance in the random walk (σ_E^2) is also small. For example, consider the special case in which there is no temporal variability in the effort, i.e., $\sigma_E^2 = 0$, then the effort is constant and fixed over the time period such that the mean log fishing mortality per age group also is constant.

The model was initialised with the recruits $N_{a_{\min},y}$ (for $y = 1, \dots, Y$) and the initial values ($N_{a,1}$ for $a = a_{\min} + 1, \dots, A$) that are parameters to be estimated (see also Gudmundsson 1994; Millar and Meyer 2000). A model for the recruitment could be integrated into this model and the parameters estimated simultaneously, for example, as a stock–recruitment relationship (Lewy and Nielsen 2003) or as a time series model (Schnute and Richards 1995), but such approaches are not considered in this paper.

The observations

The observations related to the population processes considered in this paper are the catch at age and the indices of abundance at age. The observed catches at age a in year y ($C_{a,y}$) are related to the population and fishing processes through

$$(5) \qquad C_{a,y} = \frac{F_{a,y}}{F_{a,y} + M_{a,y}} N_{a,y}(1 - \exp(-F_{a,y} - M_{a,y}))\lambda_{a,y}$$

where $\lambda_{a,y}$ is a stochastic variable with mean 1, so that mean catch at age equals the well-known deterministic relationship between the population and catch (e.g., Quinn and Deriso 1999). Here $\lambda_{a,y}$ represents random deviation between observed catches and true catches that is caused by sampling error and misspecification of the functional relationship (for a similar approach, see Lewy and Nielsen 2003). We assume that the catches are lognormally distributed and that the observations are independent between years and ages. More specifically, we assume $\lambda_{a,y} = \exp(\varepsilon_{a,y}^C - 0.5\sigma_C^2)$, where $\varepsilon_{a,y}^C$ is iid with zero mean and variance σ_C^2, so that $E(\lambda_{a,y}) = 1$ for any value of σ_C^2. The choice of a lognormal distribution for the catches implies that we assume a constant error coefficient of variation (ECV) for all ages given by ECV $= \sqrt{\exp(\sigma_C^2) - 1}$.

An alternative approach would have been to use multinomial distributions for the proportions at age (Quinn and Deriso 1999, p. 335). However, analyses of sampling error in catch-at-age data do not support multinomial distributions (S. Aanes, unpublished data).

The second source of data considered here are the indices from the research surveys. Let δ be the proportion of the year passed until the time of the survey. Then the population size at the time of the survey is $N_{a,y}^{(I)} = N_{a,y} \exp(-\delta Z_{a,y})$. The estimated survey index at age a in year y ($I_{a,y}$) is assumed to

follow a lognormal distribution with mean proportional to the abundance at the time of the survey:

(6) $\quad I_{a,y} = q_a N_{a,y}^{(I)} \exp(\varepsilon_{a,y}^I)$

$$\text{for } a_{\min}^{(I)} \leq a \leq A^{(I)}, 1 \leq y \leq Y$$

where q_a is an age-specific proportionality constant, the "catchability" of the survey, and $\varepsilon_{a,y}^I$ is a normally distributed random variable with zero mean and variance σ_I^2, allowing for errors in the observations. The error term is assumed to be independent between ages and years. The mean of the error for the catch-at-age data was adjusted to 1 to obtain the deterministic relationship for mean catch at age, while the term of the error term for the indices is $\exp(0.5\sigma_I^2)$. For the abundance indices, such an adjustment will only affect the value of q_a and is therefore not necessary to formulate explicitly.

Data sources

In this paper we use data for Northeast Arctic cod for the time period 1985–2003. We use the annual estimates of total catch at age as reported by ICES (2004) for ages 3–15 years in addition to an age-specific survey index based on a Norwegian survey in the Barents Sea covering the feeding grounds (ages 3–9 years).

The catch at age is estimated by combining biological samples with the reported landings given by the management authorities (e.g., Aanes and Pennington 2003; Hirst et al. 2004, 2005). Because of the heterogeneous fishery for many fish stocks, possibly including a variety of fleet groups and fishing over large areas, the sampling schemes become rather complex. Accordingly, Aanes and Pennington (2003) and Hirst et al. (2004) found that the uncertainties in the estimates of the Norwegian catch at age for Northeast Arctic cod were relatively large, despite intensive sampling, with ECV typically ranging from 5% to 40%, where the least precise estimates typically are for oldest fish with the lowest catches. Because of this we choose to estimate two variance components for these data: one for the catches including ages comprising the major part of the catches (σ_{C1}^2), i.e., for ages 3–10, and one for the for catches including the ages accounting for the remaining catches (σ_{C2}^2), i.e., for the ages 11–15.

The survey in the Barents Sea has been conducted annually in February since 1981 and covers the demersal fishes in the Barents Sea, which includes the feeding grounds and mainly the immature part of the Northeast Arctic cod stock (Jakobsen et al. 1997). In the routine assessments, a swept area estimate is used (ICES 2004), i.e., the estimate is integrated to an absolute estimate for the surveyed area (Jakobsen et al. 1997). Because the surveyed area may vary from year to year, we chose to use the mean catch per trawled distance as an index of abundance instead of the reported swept area index (see Appendix A) to minimize the potential effect of year-to-year variations in surveyed area. We considered cod that were 3–9 years old.

Estimation of parameters

Catch-at-age data do not, in general, contain information about natural mortality, although it can estimate the total mortality ($Z_{a,y}$) under certain conditions (see, e.g., Quinn and Deriso 1999, p. 318). Indices of abundance can estimate the age-specific total mortality if the relative differences in age-specific catchability are known (substituting the mean value, eq. 6, into eq. 1 and solving with respect to $Z_{a,y}$ yields

$$Z_{a,y} = \log(N_{a,y}/N_{a+1,y+1})$$

$$= \log([q_{a+1} E(I_{a,y})]/[q_a E(I_{a+1,y+1})])$$

If the relative differences in catchabilities are unknown, then the estimates of total mortality from surveys will be confounded with estimates of catchabilities. With a similar argument for the age-specific total mortalities, the age-specific catchabilities in the surveys could be estimated. If there is a lack of knowledge of either of the two, then the prospects of estimating age-specific natural mortality is poor without any additional information or, alternatively, using strong prior information on the parameters.

The set of parameters to be estimated is ($N_{a_{\min},1},..., N_{a_{\min},Y}$, $N_{a_{\min},+1,1},..., N_{A,1}, m_{a_{\min}},..., m_A, \sigma_M^2, \sigma_\xi^2, f_{a_{\min}},..., f_{A*}, \sigma_F^2, \sigma_E^2$) for the population dynamical process, σ_{C1}^2 and σ_{C2}^2 for the observed catches, and ($q_{a_{\min}^{(I)}},..., q_{A^{(I)}}, \sigma_I^2$) for the abundance indices from the survey. We chose vague prior distributions for most parameters, whereas the prior distributions for the parameters describing the natural mortality and the variance in the random walk (eq. 4) were chosen more informatively (see Appendix B for details).

To sample from the posteriors, we used the software package WinBUGS (Spiegelhalter et al. 1996) that uses MCMC methods to simulate the conditional distributions. Because this is an iterative simulation procedure that does not sample from the correct posteriors until convergence is reached, a certain number of iterates must be discarded before keeping the samples ("burn-in"). A variety of methods for assessing the convergence do exist (see, for example, Gelman et al. 2004), whereas we have examined this by starting three parallel Markov chains, with different (overdispersed) starting points, and applied the scale reduction factor (Gelman et al. 2004) together with visual inspections of the chains. The scale reduction factor measures the variability within and between the sequences and declines to 1 as the number of iterations approaches infinity. It is recommended that this factor should be smaller than 1.1 for all parameters for accepting convergence. Because samples from Markov chains per definition depend on earlier samples in the sequence, i.e., they are autocorrelated, it is necessary to run the Markov chains for a sufficiently long time to cover the entire posterior distribution. To reduce the number of iterations necessary to capture the entire distribution, it is therefore useful to thin the sequence by keeping only every kth iterate after convergence is obtained.

As expected, fitting the full model was not successful, which was evident from the lack of convergence of the Markov chains for the parameters, such that we were not able to estimate the posterior distributions of the parameters without using more informative priors on the age-specific

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mortalities. With the modification that natural mortality for ages above the maximum age available in the surveys (9 years) was equal to that below this age, that is, $M_{a,y} = M_{9,y}$ for $a \geq 9$, the full model was fitted successfully regarding convergence of the parameters. However, the age-specific component of the natural mortality (m_a) and the age-specific selection in the fishing mortality (f_a) were highly correlated (close to 1), indicating that the model was overparameterised. Fitting the model to simulated data sets (see next section) confirmed the problems in separating those parameters. The correlations between f_a and the age-specific catchability in the surveys (q_a) and m_a and q_a were also rather high. To overcome problems with identifiability of the parameters, natural mortality was set as known and constant 0.2 for ages 10 years or older. For ages below 10 years old, the mean log natural mortality was set as constant, that is, $m_a = m$ for $3 \leq a \leq 9$.

For each Markov chain, we found that a burn-in of 20 000 iterates ensured convergence, and by keeping 334 samples of each parameter with a thinning of 60, yielding a total of 1002 samples per parameter, the posterior distributions was sufficiently well approximated, i.e., the percentiles in the distributions were stable. The total number of samples per parameter was then 120 120.

Simulation from the model

To evaluate the model fit and parameter estimates, we simulated both the population process and observations using the estimated parameters, analogous to ordinary parametric bootstrapping, forming replicates of both the population process and data. Each replicate of population and observations was obtained as follows. The population process was simulated with the same numbers of ages as the original data. It is necessary to generate the recruits each year. The model does not include a model for the recruits, which are considered as parameters. However, a stock–recruitment relationship is implicitly given as the spawning stock size can be estimated using the proportion mature at age. In this way we model the stock–recruitment relationship as the Ricker function, i.e.,

$$N_{a_{\min}, y} = \alpha S_{y-a_{\min}} \exp(-\beta S_{y-a_{\min}}) \exp(\varepsilon_{a,y}^s)$$

where α and β are positive parameters, S_y is the spawning stock size in year y, and the $\varepsilon_{a,y}^s$s are iid normally distributed with zero mean and variance σ_S^2. The function was fitted to the posterior samples of the spawning stock size and the corresponding posterior samples of the recruits 3 years later using maximum likelihood. Each posterior sample of spawning stock size is estimated by the sum of the estimated number of mature individuals in each age group. We used the average of the annual estimates of proportion mature at age reported by ICES (2004) for the time period 1985–2003 to estimate the number of mature individuals, i.e., the proportions are constant for each age. The number of recruits was simulated by sampling at random from the residuals of the fit. To start the simulation process, it is necessary to initialise the process by setting the spawning stock size in some years in order to generate all initial values (see The population dynamical model), and we chose the initialisation period equal to the maximum age, i.e., the number of years needed for the process to generate the spawning stock itself. We used the average estimated spawning stock size as the initial value for the initialisation period.

The fishing and natural mortalities were simulated by their specified stochastic processes (eqs. 2–4) using the parameter estimates obtained by fitting the model to the data. We notice that even though we set the natural mortality as constant at 0.2 for the ages not included in the survey data when fitting the model to the observations, we simulate natural mortality according to its process (eq. 2) for all ages in the population. The random walk, modelling the log fishing effort (eq. 4), is not a stationary process and may thus produce unrealistically low or high fishing mortality rates over longer periods of time. To avoid this, we kept the fishing effort constant at 0 during the initialisation period and simulated as a random walk thereafter according to eq. 4.

Corresponding observations were then generated by simulating from the observation models (eqs. 5 and 6). The dimensions of simulated data sets are kept the same as those of the original data sets.

Results

The correlation among posterior samples of some of the parameters is shown (Fig. 1). The f_as are positively correlated with the q_as, decreasing with age and difference in age (the largest correlation is 0.88 for age 3), whereas both are negatively correlated with m, also with an absolute value that decreases with age (Fig. 1). Both m and σ_M^2 and m and σ_ξ^2 are negatively correlated (–0.31 and –0.58, respectively). The correlation between the other parameters is weaker.

Estimating stock size and natural mortality

The estimates of the total population sizes for the time period 1985–2003 are shown (Fig. 2). The estimates showed rather large temporal fluctuations, with a mean ranging from more than five billion individuals in 1986 to below one billion in 1990. The estimated mean total population sizes are higher, on average, than those obtained by the Arctic Fisheries Working Group (AWFG; Fig. 2). Although the patterns in the temporal fluctuations were similar, the range of variation was smaller in the AFWG series (CV = 0.26) than in the corresponding mean for estimated population size (CV = 0.42). The annual variation in ECV in the estimates of the total population size ranged from 20% to 40% (i.e., the standard deviation of the posterior divided by the mean over the time series), but each posterior trajectory of total stock size was very similar (the average correlation among all pairs of samples of total stock size trajectories is 0.90)

The estimated mean annual natural mortality rate for the ages 3–9 years also showed large temporal fluctuations, from below 0.2 to above 0.7, and is on average 0.36, although the estimates were rather imprecise (Fig. 3a). The component accounting for the majority of the fluctuations in natural mortality was caused by year-to-year variability, giving a high correlation within years (between 0.5 and 0.9; Table 1) for ages 3–9 years.

Fig. 1. Pairwise plots of parameter estimates for log selectivity in fishing mortality for ages 3 and 10 ($\hat{f}_3$ and $\hat{f}_{10}$, respectively), log catchability in the survey for ages 3 and 9 ($\hat{q}_3$ and $\hat{q}_9$, respectively), log mean natural mortality (m), and the variance components in natural mortality ($\hat{\sigma}_M^2$ and $\hat{\sigma}_\xi^2$). The corresponding linear correlation coefficient is given in the lower diagonal.
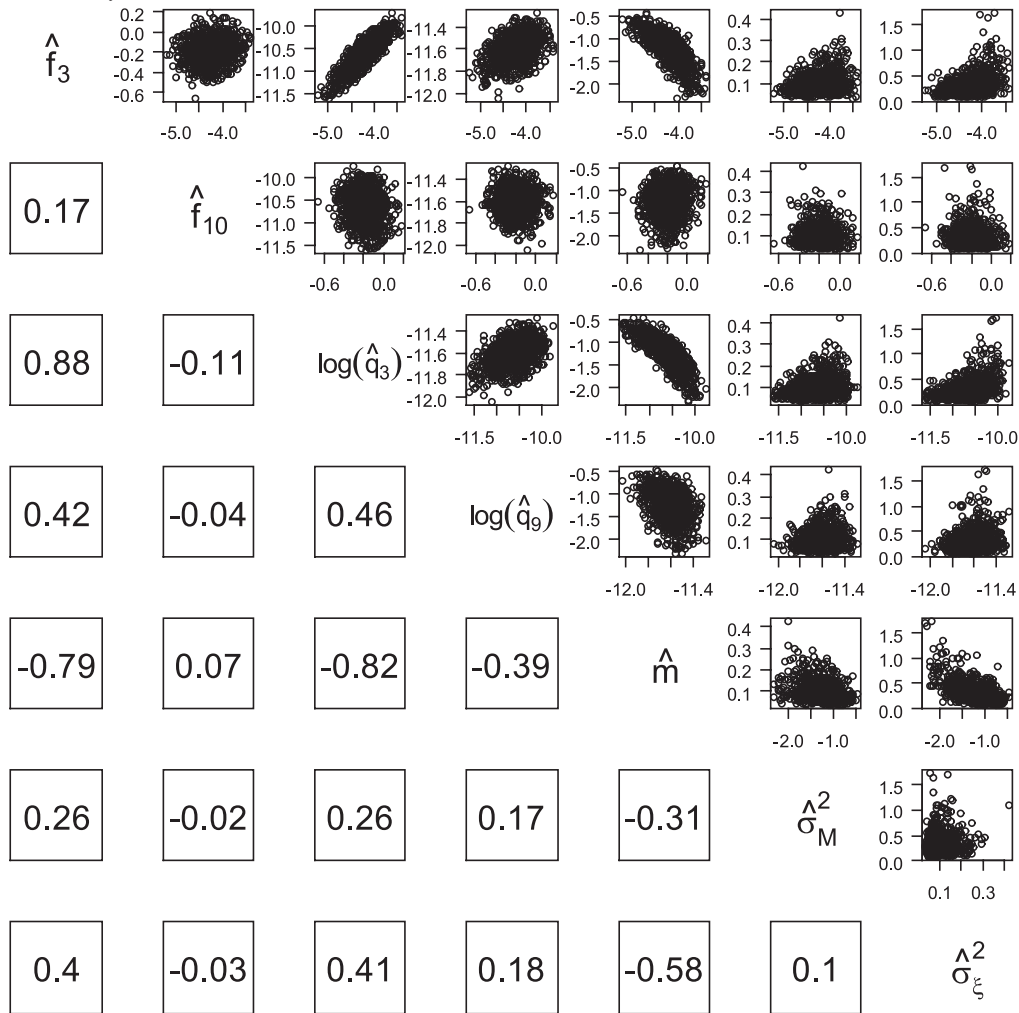
Age-specific dynamics

The ages 5–10 years comprised the major proportion of the total annual landings of cod in the Barents Sea (ICES 2004). The mean annual fishing mortality for ages 5–10 years shows the same temporal dynamics as the one from the AFWG (ICES 2004) (Fig. 3b). The temporal variability in these estimates is slightly smaller than that from the estimates from the AFWG. The estimated variance component for the process for the fishing mortality σ_F^2 (in eq. 3) is small (Table 1); thus, the deviation from the additive model for the log fishing mortality is rather small. Also the estimated effort employed by the fishing fleet changes relatively little from year to year, shown by a low estimate of the variance in the random walk for the log fishing effort (σ_E^2 in eq. 4; Table 1).

The estimates of the variances for the input data correspond to an ECV of approximately 40% for the indices from the Barents Sea, 30% for the catch at age (ages below 11 years), and above 100% for catch at age for fish older than 11 years. Thus, the data for ages below 11 years seem relatively precise, whereas the catch data for older fish are very imprecise, i.e., contain little information about the fluctuations in abundance for these ages.
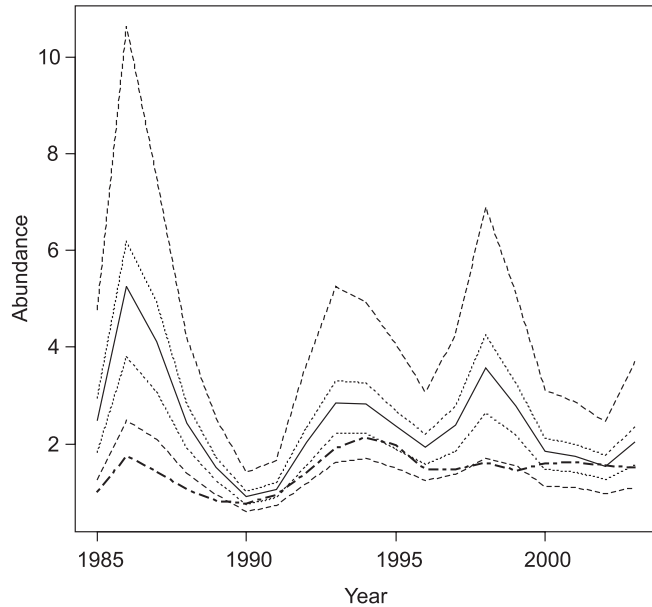
Stock size and recruitment

The relationship between spawning stock size and recruitment was fitted by the Ricker recruitment function. Large variation was found around the estimated stock–recruitment relationship (Fig. 4) because of the variability in the fitted values. The fit was used in the simulations to generate recruits given the spawning stock and did reproduce both the average abundance of the total stock and the estimated temporal fluctuations for the Northeast Arctic cod.

Simulations of fluctuations in stock size

By simulations it is evident that the fitted model estimates the total stock size very well (Fig. 5a), although the large stock sizes are slightly overestimated and small stock sizes are underestimated. By tracing the age-specific stock size, the model underestimated the actual number of recruits by an average of 15% (not shown). The magnitude of the bias decreased with age, resulting in overestimating the number

Fig. 2. The estimated total population size ($\times 10^{-9}$) of Northeast Arctic cod (*Gadus morhua*) age 3 years and older for the years 1985–2004 (solid line). The uncertainties in the estimates are shown by the 50% (dotted lines) and 95% (broken lines) credibility sets. The bold broken line represents the estimates from the Arctic Fisheries Working Group (ICES 2004).
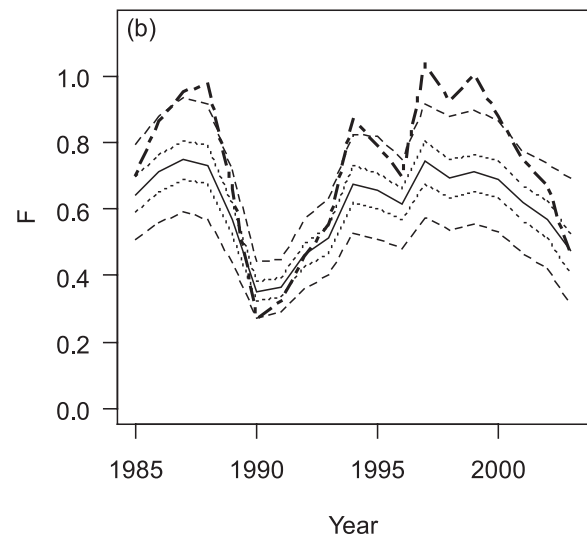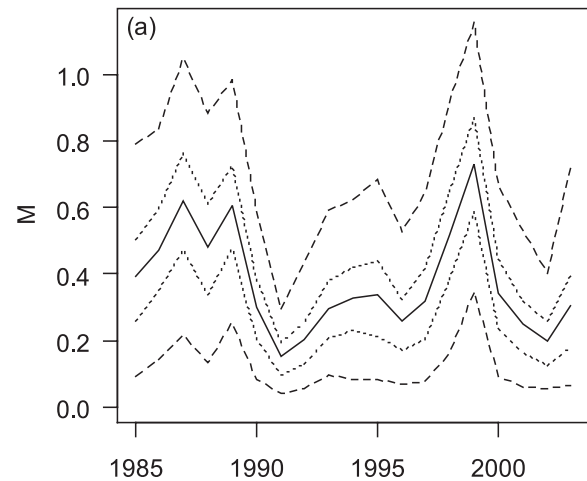

Fig. 3. The estimated annual mortality rates for the Northeast Arctic cod (*Gadus morhua*) stock for the years 1985–2003. (*a*) The estimated mean natural mortality rate for ages 3–9 years (solid line). The uncertainties in the estimates are shown by the 50% (dotted lines) and 95% (broken lines) credibility sets. (*b*) The estimated mean fishing mortality rate for ages 5–10 years (solid line). The uncertainties in the estimates are shown by the 50% (dotted lines) and 95% (dashed lines) credibility sets. The bold broken line represents the estimates given by the Arctic Fisheries Working Group (ICES 2004).

of fish in the oldest age class by about 15%. This is in agreement with Fig. 5*a* because a large total stock is dominated by young fish. Each replicate of process and corresponding data yields a correlation between the simulated time series of total population size and the corresponding estimated total population size. The mean correlation was 0.93 (95% credibility set is (0.79, 0.99)) (slightly higher than the correlation between the estimated and corresponding simulated total stock size independent of age as shown in Fig. 5*a*), showing that a high degree of the temporal fluctuations is captured by the model. The mean of the mean annual log natural mortality and the year-to-year variability (σ_ξ^2) were underestimated (Table 1; Fig. 5*b*). Accordingly, the fluctuation in natural mortality was underestimated, resulting in overestimation of small values with a bias that decreases to underestimate large values of natural mortality (Fig. 5*b*). The variance component σ_M^2 in natural mortality was overestimated, and because the unconditional mean is given by $\exp(-m + 0.5(\sigma_M^2 + \sigma_\xi^2))$, the mean of the natural mortality rate was underestimated by 20%. The level of fishing mortality independent of age was also very well estimated by the model with little bias (Fig. 5*c*). The age-specific fishing mortality was overestimated but the bias decreased with age (not shown). The relative bias for the mean fishing mortality for the ages 5–10 was about 10%.

The simulations showed that the 95% credibility sets for the estimated natural mortality and fishing mortality across ages and years both had an estimated coverage of 96.4%. Similarly, the estimated coverage for the estimated population sizes across ages and years was 95%.

We examined the ability of the model to estimate fluctuations in natural mortality outside the range of the estimated

parameters for Northeast Arctic cod. In all cases we set the natural mortality within a year constant across ages, and all variability is due to temporal fluctuations. We considered five different scenarios: (*i*) constant natural mortality, but at different levels, (*ii*) linear increase in natural mortality over time, (*iii*) linear decrease in natural mortality, (*iv*) cyclic variations in natural mortality over time, and (*v*) stochastic variations in *M* independent between years according to a uniform distribution $U(a, b)$ for different *a* and *b*. All other population processes and corresponding observations were simulated as previously described.

In general, the results are in agreement with the previous simulations. We found that small values of natural mortality

Table 1. Estimated population parameters for the model fitted to Northeast Arctic cod (see text): the mean, median, and 2.5% and 97.5% percentiles from the posterior distributions and the mean relative bias.

Parameter	Mean	Median	2.5% percentile	97.5% percentile	Mean relative bias (%)
m	−1.216	−1.171	−1.983	−0.689	−40.0
σ_M^2	0.097	0.086	0.045	0.212	48.7
σ_ξ^2	0.311	0.266	0.103	0.825	−31.6
r_M	0.734	0.747	0.455	0.911	−23.3
σ_I^2	0.143	0.141	0.101	0.194	11.5
σ_{C1}^2	0.073	0.072	0.050	0.106	33.8
σ_{C2}^2	0.758	0.749	0.547	1.032	−6.5
σ_F^2	0.039	0.038	0.025	0.057	40.9
σ_E^2	0.035	0.031	0.014	0.077	−6.4

Note: Mean log natural mortality, m; variance in log natural mortality, σ_M^2; covariance in log natural mortality, σ_ξ^2; correlation within year in log natural mortality, r_M; variance in log index from the Barents Sea, σ_I^2; variance in log catch at age for ages 3–10 years, σ_{C1}^2; variance in log catch at age for ages 11–15 years, σ_{C2}^2; variance in log fishing mortality, σ_F^2; and variance in the random walk for the log effort in fishing mortality, σ_E^2. The estimated relative bias (in percent) for the parameters is shown in the rightmost column and is based on refitting the models to 100 replicates of simulated data (see Fig. 5).

Fig. 4. The estimated mean recruitment ($\times 10^{-9}$) of 3-year-old Northeast Arctic cod (*Gadus morhua*) as a function of the estimated spawning stock three years earlier. The relationship is estimated by fitting the Ricker function to the posterior samples of the spawning stock and recruits. The solid line shows the resulting mean, and the dotted and broken lines are the corresponding 50% and 95% credibility sets for the mean recruitment, respectively.
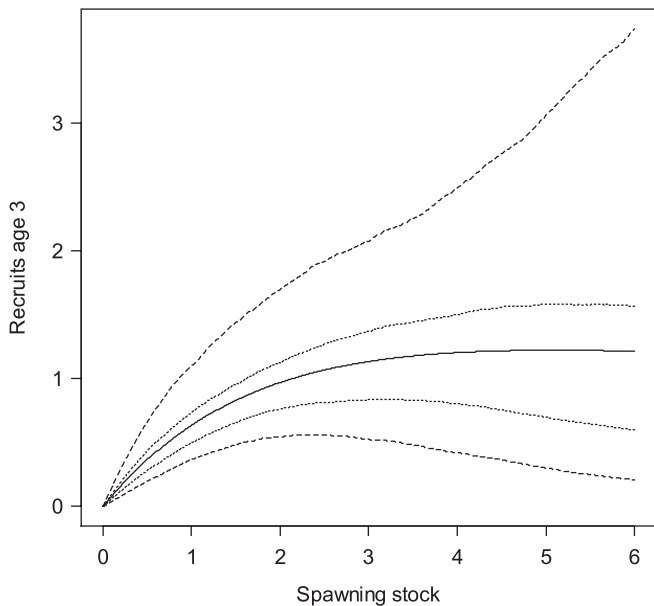
were overestimated, whereas large Ms were underestimated, and vice versa. Thus, there is a consistent relationship between bias in M and bias in stock size. The relationship between bias in M and F is less consistent, although there seem to be a tendency for a negative relationship between the two, i.e., if M is underestimated, then F is overestimated. If considering the estimated temporal fluctuations compared with the simulated fluctuations rather than the absolute dif-

ferences, we find that in all instances the estimated fluctuations in abundance are highly correlated with the simulated fluctuations (Table 2). The estimated expected correlation in the different scenarios ranges from 0.90 to 0.99, in which the correlation decreases with increasing variability in M. If the variability in temporal variations is sufficiently high, the estimated temporal variability is in close agreement with the simulated variability, although the variability is underestimated. The fluctuations in fishing mortality are in general better captured than the fluctuations in the natural mortality (higher correlations), and also here the temporal variability is underestimated, although to a lesser degree than that of the natural mortality.

Discussion

In this paper we have shown that it is possible to separate some elements of the stochastic natural and fisheries mortality by using catch-at-age data and survey indices. The major finding is that we can estimate the temporal dynamics in natural mortality, but that it is difficult to estimate the absolute value of this parameter. Also, fluctuations in stock size of Arctic cod in the Barents Sea were found to be closely related to temporal variation in natural mortality. Not surprisingly, the assessment of fish stock size would hence strongly benefit from more precise knowledge about the natural mortality.

It was not possible to estimate all parameters in the model without using any information in the prior distribution for some of the parameters (e.g., uniform prior distribution over a wide range). More specifically, the parameters most difficult to estimate were the variances in log natural mortality (σ_M^2) and log fishing mortality (σ_F^2). We therefore had to carefully select appropriate prior distributions restricting the values to a realistic range. This was also the case for the mean log natural mortality (m), although to a lesser extent than the former. We notice that the posterior distributions of the parameters do not reproduce the respective prior distribu-

Fig. 5. Comparisons of the simulated population process using the parameter estimates obtained by fitting the model to data for Northeast Arctic cod (*Gadus morhua*) with the estimates found by refitting the model to the corresponding simulated data for (*a*) annual total population size (*N*), (*b*) mean annual natural mortality ages 3–9 years (*M*), and (*c*) annual mean fishing mortality for ages 5–10 years (*F*). The solid lines are nonparametric fits of the data points to display the trend, the broken lines are the one-to-one mapping to illustrate deviation from the actual values, and the respective correlations (*r*) are shown in the figures. The results are based on refitting the model to 100 replicates of data sets. Each point represent an annual estimated mean versus the corresponding simulated mean, and each simulated data set is of length 19 years, thus each figure includes 1900 points.
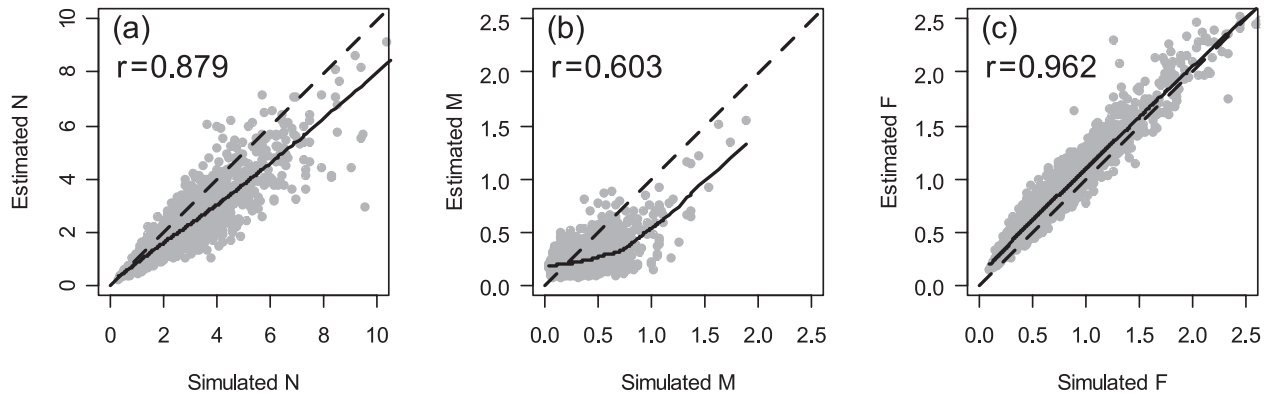

Table 2. Estimated mean correlation between temporal dynamics in estimated and simulated total stock size $(\mathrm{cor}(\hat{N}, N))$, natural mortality $(\mathrm{cor}(\hat{M}, M))$, and average annual fishing mortality for ages 5–10 years $(\mathrm{cor}(\hat{F}, F))$ and estimated mean ratio of coefficient of variation (CV) of fluctuations in estimated to simulated CV of total stock size $(\mathrm{CV}(\hat{N})/\mathrm{CV}(N))$, natural mortality $(\mathrm{CV}(\hat{M})/\mathrm{CV}(M))$, and fishing mortality $\mathrm{CV}(\hat{F})/\mathrm{CV}(F)$ for different scenarios of simulated natural mortality.

Scenario for natural mortality	$\mathrm{cor}(\hat{N},N)$	$\mathrm{cor}(\hat{M},M)$	$\mathrm{cor}(\hat{F},F)$	$\dfrac{\mathrm{CV}(\hat{N})}{\mathrm{CV}(N)}$	$\dfrac{\mathrm{CV}(\hat{M})}{\mathrm{CV}(M)}$	$\dfrac{\mathrm{CV}(\hat{F})}{\mathrm{CV}(F)}$
$M_{a,y} \equiv M = 0.01$	0.98	—	0.93	1.04	—	0.98
$M_{a,y} \equiv M = 0.2$	0.98	—	0.94	1.01	—	0.89
$M_{a,y} \equiv M = 0.5$	0.95	—	0.94	0.97	—	0.78
$M_{a,y} \equiv M = 0.7$	0.98	—	0.92	1.02	—	0.68
$M_{a,y} \equiv M = 1.0$	0.99	—	0.91	0.97	—	0.64
$M_{a,y} = M_y = (1/18)(y - 1)$	0.95	0.84	0.72	1.13	0.85	0.91
$M_{a,y} = M_y = (1/18)(19 - y)$	0.98	0.84	0.89	0.93	0.84	0.96
$M_{a,y} = M_y = 0.5(\sin(\pi y/4) + 1)$	0.90	0.91	0.81	1.16	0.69	0.90
$M_{a,y} = M_y = 0.25(\sin(\pi y/8) + 1)$	0.92	0.79	0.88	1.04	0.67	1.08
$M_{a,y} = M_y \sim U(0,1)$	0.93	0.72	0.90	0.96	0.55	0.82
$M_{a,y} = M_y \sim U(0,0.5)$	0.93	0.49	0.92	0.98	0.31	0.93
$M_{a,y} = M_y \sim U(0.1,0.3)$	0.97	0.17	0.94	1.03	0.38	0.91

Note: Scenarios considered: constant natural mortality at different levels (rows 1–5); systematic increase in natural mortality from 0 to 1 over 19 years (row 6); systematic decrease in natural mortality from 1 to 0 over 19 years (row 7); cyclic variations at different levels and with different periods (rows 8 and 9); stochastic variations in natural mortality independent between years according to a uniform distribution $U(a,b)$ for different a and b (rows 10–12). The other processes and data were simulated as for the Northeast Arctic cod case, and the same model was fitted to all simulated data sets (see text). The mean correlation and ratio CV was estimated as the average over 20 replicates of simulated process and data and the corresponding estimated process.

tions, and thus, there is some information in the data for those parameters, although the signal is weak (particularly for σ_M^2). This suggests that later studies should explore the strength of the signal for these parameters to derive appropriate priors beyond the method we have chosen to derive these priors. The other parameters in the model were not sensitive to the choice of prior distribution provided that the distribution was restricted to reasonable intervals. One of the strengths of the Bayesian approach is that it makes it possible to reflect our prior knowledge by a distribution, instead of setting unknown parameters in a model as constants. In situations in which some parameters in a model depend on

the prior distribution, the sensitivity of the exact choice of prior distribution should be investigated (e.g., mean, variance, and type of distribution). Such detailed and systematic analysis is not done here and should be subject for further study. However, preliminary results suggest that the estimated temporal dynamics is not sensitive to other choices of reasonably chosen prior distributions but may cause changes in the estimated mean log natural mortality, which again affects the perceived absolute population size.

By using data from the Northeast Arctic cod stock, we have shown that this model type can estimate the fluctuations in population size, as well as separate the stochastic

components in mortality provided that we accept to use some prior information about some specific parameters. The precision in the estimates of total stock size (ECV is 20%–40%) appeared comparable to reported figures based on similar methods (Lewy and Nielsen 2003). Assuming that the natural mortality was a known constant or, analogously, choosing highly informative prior distributions for these parameters resulted in a dynamical pattern more closely related to the estimates provided by the AFWG. Obviously, the estimates will be less uncertain (ECV between 5% and 20%) if one assumes that the natural mortality is known. However, the samples from the posterior distribution of stock size – time series were highly correlated (the average correlation among all pairs of samples of stock size trajectories is 0.90), i.e., the dynamical pattern is nearly identical, but the absolute stock size differs. This indicates that the estimates are uncertain as a result of the same factor. Thus, the uncertainty in the estimated temporal fluctuations is lower than it appears in Fig. 2. Accordingly, there was a high correlation between the estimated abundance and the corresponding simulated data. Thus, gathering data for more precise estimates of natural mortality will greatly improve the precision in the estimates of the stock size.

The estimates of stock sizes and fishing mortalities are comparable with existing estimates provided by existing methods (ICES 2004), although this method shows different levels of variability. The estimates provided by the AFWG in 2004 for the population size and fishing mortality are in some years outside the estimated 95% credibility sets, but because these estimates do not provide any level of uncertainty, it is difficult to judge whether they are significantly different or not.

Our simulations revealed that our method gave poor estimates of the level of natural mortality that resulted in uncertain estimates of the total population size. This indicates that information about natural mortality obtained from other sources such as capture–recapture studies must be included in the model to obtain reliable estimates of total population size. Another possibility is to use a more strict Bayesian approach to put stronger constraints on the variation in the prior distributions of the natural mortality (m). Our method gives different estimates of total population size than by assuming a constant natural mortality of 0.2 with an additional mortality caused by cannibalism as employed by the AFWG (ICES 2004) for the cod. The resulting temporal dynamics in natural mortality is in poor agreement with the estimates found here, and we estimate higher natural mortality (mean of 0.36) with larger temporal fluctuations. This is the main reason for estimating the stock size to a higher level with larger temporal variability than the official estimates. Fortunately, our method seems to estimate annual fluctuations in the natural mortality quite well, enabling estimation of temporal fluctuations in stock size quite well. The high correlation between ages within year in natural mortality suggests that the major component causing fluctuations in this mortality is year-to-year variability. Empirical evidence from a variety of taxa suggests that temporal variation in life history traits with high sensitivities (Caswell 2001), such as adult survival rates in relatively long-lived species such as the Arctic cod, should be small (Pfister 1998; Sæther and Bakke 2000; Gaillard and Yoccoz 2003). Our findings of a large

variability in natural mortality between years then may be primarily caused by discarding and black landings (ICES (2005), Myers et al. (1997), and Zeller and Pauly (2005) and references therein), or alternatively it may be caused by variability in rates of predation by sea mammals.

Another problem was to obtain reliable estimates of the variance in natural mortality (σ_M^2) because of a negative relationship ($r = -0.31$) between σ_M^2 and m. This may be caused by variation in m that will induce fluctuations in age structure that will give autocorrelations in the process (Lande et al. 2006) and hence affect the estimates of σ_M^2.

In comparing the estimated precision levels in the catch data and the indices from the survey, it is apparent that, within this model, the catch data for the ages 3–10 years are only slightly more precise than those of the survey, whereas the catch data for the ages 11–15 years were very imprecise. This shows that the parameter estimates rely mainly on the data for ages up to 10 years and little on the ages above. Hence, leaving out the data for the oldest fish would probably not result in significant changes for the estimates. The estimated precision levels of the input data contain both sampling error and process error and are confounded within this model. If the sampling error is known beforehand, then subject to some assumptions, the total error is the sum of sampling and process error (Lewy and Nielsen 2003). In the present paper, the sampling error (not shown) for the Norwegian catches were, on average, larger than the process error for all catches (estimated by modelling the sampling schemes; see Aanes and Pennington (2003) and Hirst et al. (2004, 2005)). However, because of the lack of data from other than Norwegian catches, we can not exclude the possibility that process error may be of more significant importance than the error related to sampling (see Lewy and Nielsen (2003) for an example on North Sea plaice).

We assumed that the errors in the input data were independent and identically distributed across ages and years. The effect of violating this assumption is not examined, but in general, this could cause biases in the estimates, with a magnitude depending on the magnitude of correlation at age within year and the relative differences in precision between ages. The magnitude of this potential problem could be explored as in Myers and Cadigan (1995a; 1995b), who allowed the survey indices to be correlated within years and quantified by simulations similar to what is done in this paper, or alternatively one could try to estimate the entire covariance matrix. Estimating the entire covariance matrix would probably lead to overparameterisation of the model, and it would therefore be advantageous to parameterise the covariance matrices with as few parameters as possible to avoid this problem. Lillegård et al. (2005) examined the process noise for the spawning stock of the Norwegian spring spawning herring and found only a very small temporal correlation, which was mainly generated by a small temporal correlation in temperature.

The model was able to reproduce simulated data. Although some parameter estimates were biased, the estimates of the most important figures — the total stock size, natural mortality, and fishing mortality — were very accurate with relatively small biases. The reported biases for stock size and fishing mortality agree with the estimated biases found by Lewy and Nielsen (2003), and the estimated coverage of

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the credibility sets was close to the true probability. For simulation purposes, we fitted the stock–recruitment function to the posterior estimates of spawning stock size and recruits. The fit showed large variability around the mean, which could have been caused by factors such as process error and (or) environmental noise (Mann and Drinkwater (1994), Ottersen et al. (2001), and Myers (2002) and references therein). The fitted function is, however, in agreement with other fits (e.g., Myers et al. 1996, 1997).

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Appendix A. Survey indices.

Table A1. Stratified average catch in numbers per towed distance for ages 3–9 for the annual survey in February for demersal fishes in the Barents Sea (Jakobsen et al. 1997) for the years 1985–2003.

| Year | Age | | | | | | |
	3	4	5	6	7	8	9
1985	27.04	19.74	3.33	1.46	0.54	0.10	0.01
1986	130.37	29.68	11.83	1.72	0.23	0.02	0.01
1987	43.91	68.32	9.56	3.13	0.31	0.11	0.00
1988	19.79	10.37	24.36	3.08	0.60	0.07	0.01
1989	4.90	9.51	5.48	13.74	1.42	0.17	0.02
1990	2.95	4.25	4.96	3.15	4.09	0.29	0.04
1991	3.60	2.65	2.35	2.20	1.23	1.27	0.06
1992	25.84	10.19	3.44	2.34	1.40	0.73	0.52
1992	29.12	18.56	8.48	1.83	0.91	0.49	0.26
1994	23.81	30.99	14.30	4.93	0.94	0.22	0.12
1995	18.91	17.00	20.14	6.20	1.47	0.22	0.05
1996	10.06	10.11	11.95	11.09	2.63	0.31	0.04
1997	18.10	6.83	8.07	7.19	3.89	0.71	0.13
1998	43.83	28.42	6.32	4.37	2.84	1.33	0.19
1999	21.98	23.16	10.34	2.33	1.13	0.49	0.11
2000	17.03	9.25	8.54	2.51	0.41	0.18	0.09
2001	14.01	14.66	7.57	3.76	0.85	0.10	0.05
2002	7.28	10.80	9.91	4.49	1.50	0.23	0.03
2003	23.35	10.57	10.86	8.65	2.40	0.59	0.12

Note: The data are stratified according to the actual spatial survey design the given year. The catches before 1989 are adjusted according to the change from Bobbins to Rockhopper gear using established correction factors (Godø and Sunnanå 1992).

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Appendix B. Prior distributions.

The prior distributions for the parameters in the model described in Model are chosen as follows.

For the log recruits ($\log(N_{a_{\min},y})$, $y = 1,...,Y$), the log initial values ($\log(N_{a,1})$, $a = a_{\min} ,..., A$), the log catchabilities in the surveys ($\log(q_a)$, $a = a_{\min}^{(I)},..., A^{(I)}$), and the log fishing selectivity ($\log(f_a)$, $a = a_{\min} ,..., A^*$), we chose normally distributed priors with variance 1000, and means 10, 10, –5, and –1.5, respectively. The mean in the distributions are arbitrarily chosen, and the posterior distribution does not depend on these choices.

The estimates of fishing mortality given in ICES (2005) shows age-specific temporal variation in fishing mortality corresponding to a coefficient of variation of slightly above 0.2 for the time period and age groups considered in this paper. This corresponds to the variance in the lognormal distribution being ≈0.04. Therefore, we parameterise the inverse gamma for the variance in the random walk modelling the fishing effort σ_E^2 such that the mean is 0.04 and variance is 0.01, and consequently 95% of the probability mass of the prior distribution is between ≈0 and 0.17 (see Figs. B1*a* and B1*b*).

The prior for the random variability in fishing mortality (σ_F^2) is chosen the same as for the variance components in natural mortality (see rationale below).

The variance in natural mortality rarely exceeds 0.04 (Sæther et al., unpublished). Because the natural mortality is modelled as a lognormally distributed process, i.e., $M_{a,y} \sim \text{LN}(\mu, \sigma^2)$, the variance of M is given by $(E(M))^2 (e^{\sigma^2} - 1)$. Then, given that $E(M) = 0.2$, the variance of the mortality rate is constrained to $0.04 > 0.2^2 (e^{\sigma^2} - 1) \sim \sigma^2 < \log(2)$. To achieve this, we chose to parameterise the inverse gamma for both components in natural mortality, σ_ξ^2 and σ_M^2, such that the mean is 0.172 with variance 0.017. Then for each component, 95% of the probability mass of the prior distribution is in the interval $(0.05, 0.5)$ (see Figs. B1c and B1d). This choice results in prior distribution of median M with 95% probability mass in the interval $(0.03, 1.42)$.

The priors for the variance for the error distribution for the input data, σ_{C1}^2, σ_{C2}^2, and σ_I^2, were parameterised such that both the mean and standard deviation are 0.5, and consequently 95% of the probability mass of the error distribution is in the interval $(0.02, 2)$ (see Figs. B1e and B1f).

Fig. B1. Prior distribution is gamma for the inverse variance or equivalently inverse gamma for the variance. (*a* and *b*) The prior distribution of the variance in the random walk modelling the year to year changes of log fishing mortality (σ_E^2); (*c* and *d*) the random variation in fishing mortality (σ_F^2) and the variance components for the natural mortality (σ_ξ^2 and σ_M^2); (*e* and *f*) the prior for the variance in the error distributions for the input data (σ_{C1}^2, σ_{C2}^2, and σ_I^2).

(a) Gamma, E(x)=44.049, Var(x)=891.518

(b) Inverse Gamma, E(x)=0.042, Var(x)=0.01

(c) Gamma, E(x)=7.936, Var(x)=16.837

(d) Inverse Gamma, E(x)=0.172, Var(x)=0.017

(e) Gamma, E(x)=3, Var(x)=3

(f) Inverse Gamma, E(x)=0.5, Var(x)=0.25