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Gaining information from commercial catch for a Bayesian two-stage biomass dynamic model: application to Bay of Biscay anchovy

Leire Ibaibarriaga[1]*, Carmen Fernández[2], and Andrés Uriarte[3]

[1]AZTI-Tecnalia, Txatxarramendi Ugartea z/g, 48395 Sukarrieta, Spain
[2]IEO, Centro Oceanográfico de Vigo, Cabo Estai-Canido, Apartado 1552, 36200 Vigo, Spain
[3]AZTI-Tecnalia, Herrera Kaia Portualdea z/g, 20110 Pasaia, Spain

*Corresponding Author: tel: +34 94 6574000; fax: +34 94 6572555; e-mail: libaibarriaga@azti.es.

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A two-stage biomass dynamic model for Bay of Biscay anchovy is presented. Compared with the model currently applied by ICES for the assessment of that stock, the new model separates the growth and natural mortality processes and allows them to differ by age class. Stochastic equations involving the observed weights by age class in surveys are incorporated to provide information on growth rates. The fishing process is modelled separating fishing mortality into year and age-class effects in each semester, and observation equations are introduced for total catch and catch proportion by age class (in biomass) by semester. The model is first tested on simulated data, then applied to real data for the years 1987–2008. Although the results are affected by survey catchability and natural mortality assumptions, estimates of population trends, when expressed in relation to the value in a given year, are robust. The new model has significantly more parameters, requiring longer computational time for its fitting, which is done in a Bayesian context. However, it does allow the testing of different assumptions on natural mortality, which is of special interest after the recent fishery closure, and estimating new parameters, which could provide further insight on stock and fleet dynamics.

Keywords: anchovy, Bayesian, catch data, fishery closure, Markov chain Monte Carlo, natural mortality, state-space model.

Introduction

The most common fish stock assessment methods currently used are age-structured population models based on either virtual population analysis or statistical catch-at-age-type approaches (Hilborn and Walters, 1992). Catch-at-age data are essential for fitting this type of model, but the reliability of commercial data has often been questioned (Cotter *et al.*, 2004). For small pelagic fish, even if commercial catch data are reliable, the short life expectation of the fish makes following cohorts in age-structured models difficult. At the same time, their characteristic aggregating behaviour prevents the use of commercial catch per unit effort (cpue) as an index of abundance (Csirke, 1988; Pitcher, 1995). Moreover, small pelagic fish stocks are highly sensitive to environmental change and suffer large and variable natural mortality. Some of these issues are addressed by close monitoring using fishery-independent research surveys, such as with acoustics and of ichthyoplankton (Gunderson, 1993). The abundance estimates may then be used as tuning indices to fit assessment models (Barange *et al.*, 2009).

Many authors have explored models that rely less heavily on catch-at-age data (Beare *et al.*, 2005; Porch *et al.*, 2006). This is the case for Bay of Biscay anchovy (*Engraulis encrasicolus*). Its current ICES assessment is conducted by a two-stage biomass dynamic model, where commercial catches are subtracted from the stock at two time instances each year without modelling the fishing process (Ibaibarriaga *et al.*, 2008; ICES, 2009a). Alternatively, in the biomass random-effect model applied to the same stock by Trenkel (2008), catches are not considered at all, and model fitting is based solely on survey abundance indices. In both models, the population is structured into two age classes (recruits and adults), similar to the models of Collie and Sissenwine (1983), Mesnil (2003), Roel and Burtterworth (2000), and Roel *et al.* (2009), which has been demonstrated to be sufficient to track the main dynamics of the anchovy stock successfully.

Nevertheless, catch data are still considered potentially to provide useful information for Bay of Biscay anchovy. Up to 2005, when the stock was assessed using integrated catch-at-age analysis (ICA; Patterson and Melvin, 1996; ICES, 2005), catch data were especially useful in years when the abundance indices from the two research surveys (daily egg production method, DEPM, and acoustics) disagreed or were not available. The ICA model is age-structured, with fishing mortality separated into age effects and year effects, and is fitted using abundance indices from surveys and catch-at-age data. An extension that allows for five different fleets operating through the year, called seasonal ICA (SICA) has also been developed (ICES, 2005, 2009b). The results of ICA and SICA are similar for the common parameters, but the annual fishing mortality and age-selectivity estimates from ICA can be decomposed into the seasonal fishing mortality and age-selectivity estimates from SICA.

The rate of natural mortality (M) is a key parameter to describe fish population dynamics (Hilborn and Walters, 1992). However, it is difficult to separate the mortality effects attributable to natural causes (cannibalism, predation, etc.) from those attributable to fishing, so M is usually estimated from alternative sources (Vetter, 1988), and the estimate is used in stock assessment models assuming that it is known and constant over time. The other parameters are estimated relative to the assumed natural mortality. There is one situation in which abundance indices from research surveys could provide some information on M, namely in the absence of fishing. The fishery for Bay of Biscay anchovy collapsed in 2005 and was closed from then until March 2010. Although, for small pelagic stocks, natural mortality is expected to be highly variable depending on environmental conditions, some new knowledge of average M is to be expected from research surveys in recent years.

The main objective of this paper is to study whether commercial catch data (including the absence of catches during the fishery closure) can provide useful information for the assessment of Bay of Biscay anchovy. In the two-stage biomass-based model described in Ibaibarriaga *et al.* (2008), catches were assumed to occur instantaneously and were simply subtracted from the population at two time-instances each year. In the model extension developed here, catch is assumed to be continuous in time. Fishing mortality is separated by semester, representing two distinct fishing patterns. The first semester fishery consists mainly of the Spanish purse-seine fishery operating in spring, and the second semester fishery primarily includes operations of the French fleet (Uriarte *et al.*, 1996, 2008; Vermard *et al.*, 2008). Two stochastic observation equations for commercial catch (one for total catch, the other for proportion by age class, in biomass) are included per semester. In addition, rates of growth and natural mortality, which were captured by a single parameter in the two-stage biomass dynamic model in Ibaibarriaga *et al.* (2008), are considered separately and additionally split by age class. The annual intrinsic growth rates are estimated from observations, whereas rates of natural mortality are either assumed known or treated as unknown model parameters.

The model is fitted in a Bayesian framework. The performance of the new model is first tested on simulated data, then applied to real data for the years 1987–2008. Advantages and disadvantages of the new model with respect to the previous one are discussed, and gains and losses from the incorporation of observation equations for commercial catch data are summarized. The applicability of this model to other fish stocks is also evaluated.

Model description

State equations

Let $B(t, y, a)$ denote the biomass of age a at time-instant t ($0 \le t \le 1$) in year y (where age class $a+$ denotes individuals aged a and older). Recruitment in year y refers to age 1 biomass at the start of the year and is assumed to be lognormally distributed with mean μ_R and precision (inverse of variance) ψ_R, i.e.

$$\log(R_y) = \log\big(B(0, y, 1)\big) \sim \mathrm{Normal}\big(\mu_R, 1/\psi_R\big). \tag{1}$$

Biomass at age a ($a = 1, 2+$) evolves during semester j ($j = 1, 2$) as follows:

$$\begin{aligned} B(t, y, a) = B(b_{\mathrm{sem}_j}, y, a) \exp\{(G_a - M_a \\ - f(\mathrm{sem}_j, y)s(\mathrm{sem}_j, a))(t - b_{\mathrm{sem}_j})\}, \end{aligned} \tag{2}$$

where t is a time-point during the semester, b_{sem_j} denotes the beginning of the semester, G_a and M_a are the intrinsic growth and natural mortality rates at age, and $f(\mathrm{sem}_j, y)$ and $s(\mathrm{sem}_j, a)$ represent the year and age factors of the fishing mortality rate in that semester.

Two monitoring surveys, an acoustic one and a DEPM, take place at time t_{surv}. For modelling purposes, it is assumed that both surveys take place on 15 May each year ($t_{\mathrm{surv}}= 0.375$). From Equation (2), biomass of ages 1 and 2+ at survey time will be

$$\begin{aligned} B(t_{\mathrm{surv}}, y, 1) = R_y \exp\{(G_1 - M_1 \\ - f(\mathrm{sem}_1, y)s(\mathrm{sem}_1, 1))t_{\mathrm{surv}}\}, \end{aligned} \tag{3}$$

$$\begin{aligned} B(t_{\mathrm{surv}}, y, 2+) = B(0, y, 2+) \exp\{(G_{2+} - M_{2+} \\ - f(\mathrm{sem}_1, y)s(\mathrm{sem}_1, 2+))t_{\mathrm{surv}}\}, \end{aligned} \tag{4}$$

where $B(0, y, 2+)$ is the biomass surviving from the previous year, which may be computed as

$$\begin{aligned} B(0, y, 2+) = \sum_{a=1,2+} B(t_{\mathrm{surv}}, y-1, a) \exp\{(G_a - M_a)(1 - t_{\mathrm{surv}}) \\ - f(\mathrm{sem}_1, y-1)s(\mathrm{sem}_1, a)(0.5 - t_{\mathrm{surv}}) \\ - f(\mathrm{sem}_2, y-1)s(\mathrm{sem}_2, a)0.5\}. \end{aligned} \tag{5}$$

The total biomass at the time of the survey is the sum of the two age groups:

$$B(t_{\mathrm{surv}}, y, 1+) = \sum_{a=1,2+} B(t_{\mathrm{surv}}, y, a), \tag{6}$$

and the age 1 biomass proportion (BP) is given by

$$BP(t_{\mathrm{surv}}, y) = \frac{B(t_{\mathrm{surv}}, y, 1)}{B(t_{\mathrm{surv}}, y, 1+)}. \tag{7}$$

According to the Baranov catch equation (Baranov, 1918), the catch at age a (in biomass) in semester j of year y is

$$\begin{aligned} C(\mathrm{sem}_j, y, a) = B(b_{\mathrm{sem}_j}, y, a) \\ \{1 - \exp\{(G_a - M_a - f(\mathrm{sem}_j, y)s(\mathrm{sem}_j, a))0.5\}\} \\ \frac{f(\mathrm{sem}_j, y)s(\mathrm{sem}_j, a)}{-G_a + M_a + f(\mathrm{sem}_j, y)s(\mathrm{sem}_j, a)}. \end{aligned} \tag{8}$$

The total catch is the sum of the two age classes:

$$C(\mathrm{sem}_j, y, 1+) = \sum_{a=1,2+} C(\mathrm{sem}_j, y, a), \tag{9}$$

and the age 1 biomass proportion in the catch (CP) is

$$CP(\mathrm{sem}_j, y) = \frac{C(\mathrm{sem}_j, y, 1)}{C(\mathrm{sem}_j, y, 1+)}. \tag{10}$$

Observation equations

The observation equations for the survey biomass indices $B_{\mathrm{surv}}(t_{\mathrm{surv}}, y, 1+)$ and age 1 biomass proportion $BP_{\mathrm{surv}}(t_{\mathrm{surv}}, y)$ are the same as in Ibaibarriaga *et al*. (2008):

$$\begin{aligned} &\log(B_{\mathrm{surv}}(t_{\mathrm{surv}}, y, 1+)) \\ &\sim \mathrm{Normal}\left(\log(q_{\mathrm{surv}}) + \log(B(t_{\mathrm{surv}}, y, 1+)), \frac{1}{\psi_{\mathrm{surv}}}\right), \end{aligned} \tag{11}$$

$$\begin{aligned} BP_{\mathrm{surv}}(t_{\mathrm{surv}}, y) \sim \ & \mathrm{Beta}(e^{\xi_{\mathrm{surv}}} BP(t_{\mathrm{surv}}, y), \\ & e^{\xi_{\mathrm{surv}}}(1 - BP(t_{\mathrm{surv}}, y))), \end{aligned} \tag{12}$$

where for each survey surv = depm, ac (DEPM and acoustics), q_{surv} denotes the catchability, ψ_{surv} is the precision, and ξ_{surv} is related to the variance of the observation equation for the age 1 biomass proportion. In particular, the variance of $BP_{\mathrm{surv}}(t_{\mathrm{surv}}, y)$ is given by $(1 + e^{\xi_{\mathrm{surv}}})^{-1} BP_{\mathrm{surv}}(t_{\mathrm{surv}}, y)(1 - BP_{\mathrm{surv}}(t_{\mathrm{surv}}, y))$(see Ibaibarriaga *et al*., 2008, for further detail).

The total catches observed by semester C_{obs} (sem_j, y, 1+) are assumed to be lognormally distributed with the mean given by the actual catches (on a log-scale) according to the model and precision ψ_{catch}:

$$\log(C_{\mathrm{obs}}(\mathrm{sem}_j, y, 1+)) \sim \mathrm{Normal}\left(\log(C(\mathrm{sem}_j, y, 1+)), \frac{1}{\psi_{\mathrm{catch}}}\right). \tag{13}$$

The observation equation for the age 1 biomass proportion in the catch is taken as

$$CP_{\mathrm{obs}}(\mathrm{sem}_j, y) \sim \mathrm{Beta}(e^{\xi_{\mathrm{catch}}} CP(\mathrm{sem}_j, y), e^{\xi_{\mathrm{catch}}}(1 - CP(\mathrm{sem}_j, y))), \tag{14}$$

where ξ_{catch} is a parameter related to the variance of the observation equation.

In addition, the stock weights-at-age estimated from the surveys are used to include observation equations for the intrinsic growth parameter G_a:

$$G_{\mathrm{obs}}(y, a) \sim \mathrm{Normal}\left(G_a, \frac{1}{\psi_G}\right) \tag{15}$$

for $a = 1$, 2+, where $G_{\mathrm{obs}}(y, a) = \log(w_{y+1,a+1}/w_{y,a})$ is the logarithm of the weights-at-age ratio estimated from surveys in consecutive years. Basically, ages 1, 2, and 3+ are observed in the surveys, and the observations for the growth parameter at age 2+ are computed from the weights at ages 2 and 3+, using an average weighted by abundance-at-age.

All the observation equations [Equations (11)–(15)] are assumed to be independent of each other, as well as independent across years $y = 1, \ldots, Y$, age groups $a = 1$, 2+, semesters $j = 1$, 2, and surveys surv = depm, ac.

Parameters and prior distributions

The unknown parameters are the initial biomass, $B_0 = B$ (0, 1, 2+), defined as the age 2+ biomass at the start of the first year ($y = 1$), the average log-recruitment level, μ_R, the precision of the normal process for log-recruitment, ψ_R, the survey catchabilities, q_{depm} and q_{ac}, the parameters affecting the precision of the observation equations, ψ_{depm}, ψ_{ac}, ξ_{depm}, ξ_{ac}, and ξ_{catch}, the year and age components of the fishing mortality by semester, $f(\mathrm{sem}_j, y)$ and $s(\mathrm{sem}_j, a)$, the annual intrinsic growth rates by age, G_a, the precision of the observation equations of growth, ψ_G, and the annual natural mortality rates by age, M_a. Fishing mortality, which is the product of $f(\mathrm{sem}_j, y)$ and $s(\mathrm{sem}_j, a)$, can be estimated, whereas the component parameters $f(\mathrm{sem}_j, y)$ and $s(\mathrm{sem}_j, a)$ can only be estimated in relation to each other. To resolve this issue, the 2+ age-class selectivity parameters have been fixed to 1, i.e. $s(\mathrm{sem}_j, 2+) = 1$ for both semesters. Therefore, $f(\mathrm{sem}_j, y)$ corresponds to the fishing mortality of the 2+ age class. No discards or underreporting are expected, and the recorded total landings are assumed to be very close to the actual catches. Hence, the parameter ψ_{catch} is fixed at 400, which corresponds to a *CV* of 5% in the total catch observation equation (13). In a Bayesian context, a prior distribution has to be elicited for all unknown parameters. It is assumed that all are independent *a priori*, so that the joint prior distribution is the product of the individual prior distributions, which are chosen to be

$$\begin{aligned} \log(q_{\mathrm{surv}}) &\sim \mathrm{Normal}\left(\mu_{q_{\mathrm{surv}}}, 1/\psi_{q_{\mathrm{surv}}}\right), \quad \mathrm{surv} = \mathrm{depm, ac} \\ \psi_{\mathrm{surv}} &\sim \mathrm{Gamma}\left(a_{\psi_{\mathrm{surv}}}, b_{\psi_{\mathrm{surv}}}\right), \quad \mathrm{surv} = \mathrm{depm, ac} \\ \xi_{\mathrm{surv}} &\sim \mathrm{Normal}\left(\mu_{\xi_{\mathrm{surv}}}, 1/\psi_{\xi_{\mathrm{surv}}}\right), \quad \mathrm{surv} = \mathrm{depm, ac} \\ \xi_{\mathrm{catch}} &\sim \mathrm{Normal}\left(\mu_{\xi_{\mathrm{catch}}}, 1/\psi_{\xi_{\mathrm{catch}}}\right) \\ \log\left(f\,(\mathrm{sem}_j, y)\right) &\sim \mathrm{Normal}\left(\mu_f, 1/\psi_f\right), \quad j = 1, 2, \ y = 1, \ldots, Y \\ s(\mathrm{sem}_j, 1) &\sim \mathrm{Unif}(a_s, b_s), \quad j = 1, 2 \\ \log(B_0) &\sim \mathrm{Normal}\left(\mu_{B_0}, 1/\psi_{B_0}\right) \\ \mu_R &\sim \mathrm{Normal}\left(\mu_{\mu_R}, 1/\psi_{\mu_R}\right) \\ \psi_R &\sim \mathrm{Gamma}\left(a_{\psi_R}, b_{\psi_R}\right) \\ \log(G_a) &\sim \mathrm{Normal}\left(\mu_{\log(G)}, 1/\psi_{\log(G)}\right), \quad a = 1, 2+ \\ \psi_G &\sim \mathrm{Gamma}\left(a_{\psi_G}, b_{\psi_G}\right) \\ \log(M_a) &\sim \mathrm{Normal}\left(\mu_{\log(M)}, 1/\psi_{\log(M)}\right), \quad a = 1, 2+. \end{aligned} \tag{16}$$

The hyperparameters of the prior distributions and corresponding medians and 90% probability intervals are listed in Table 1. The prior distributions were centred at values that were considered realistic and chosen to have substantial but not unreasonably large dispersion. Some of the hyperparameters used in Ibaibarriaga *et al.* (2008) were modified to obtain narrower prior probability intervals. Sensitivity of the results of the previous model to the new priors was analysed and no influence was found, except for absolute population levels when all model parameters were estimated. It is especially in that case that the new prior distributions are considered more reasonable and appropriate.

Table 1. Hyperparameters specifying the prior distribution and corresponding medians and 90% central probability intervals for the model parameters.

Parameter	Hyperparameter	Median (90% probability interval)
q_{surv}	$\mu_{q_{\text{surv}}} = 0\ \psi_{q_{\text{surv}}} = 2$	1 (0.3, 3.2)
ψ_{surv}	$a_{\psi_{\text{surv}}} = 0.9\ b_{\psi_{\text{surv}}} = 0.02$	29.8 (1.7, 139.9)
ξ_{surv}	$\mu_{\xi_{\text{surv}}} = 5\ \psi_{\xi_{\text{surv}}} = 0.2$	5 (1.3, 8.7)
ξ_{catch}	$\mu_{\xi_{\text{catch}}} = 5\ \psi_{\xi_{\text{catch}}} = 0.2$	5 (1.3, 8.7)
B_0	$\mu_{B_0} = 10.3\ \psi_{B_0} = 1.0$	29 733 (5 740, 154 022)
μ_R	$\mu_{\mu_R} = 9.8\ \psi_{\mu_R} = 1.0$	9.8 (8.2, 11.4)
ψ_R	$a_{\psi_R} = 2\ b_{\psi_R} = 3$	0.6 (0.1, 1.6)
$s(\text{sem}_j, 1)$	$a_s = 0\ b_s = 2$	1.0 (0.1, 1.9)
$f(\text{sem}_j, y)$	$\mu_f = -0.9\ \psi_f = 1$	0.4 (0.1, 2.1)
M_a	$\mu_{\log(M)} = 0.2\ \psi_{\log(M)} = 5$	1.2 (0.6, 2.5)
G_a	$\mu_{\log(G)} = -0.7\ \psi_{\log(G)} = 2$	0.5 (0.2, 1.6)
ψ_G	$a_{\psi_G} = 1.5\ b_{\psi_G} = 0.1$	11.8 (1.8, 39.1)

Inference

From Bayes' theorem, the joint posterior probability density function (pdf) of the unknowns is proportional to the product of the pdfs given in Equations (1) and (11)–(16). Markov chain Monte Carlo (MCMC) techniques (Gilks *et al.*, 1996) were used to sample from the posterior distribution. The implementation was done using the software BUGS (Bayesian inference Using Gibbs Sampling; Spiegelhalter *et al.*, 1996; Gentleman, 1997; Lunn *et al.*, 2000), which can be freely downloaded from www.mrc-bsu.cam.ac.uk/bugs/. The WinBUGS development interface (Lunn, 2003) reduced run times by about a factor of 20 (Lunn *et al.*, 2009). Analysis of the results was conducted in R (www.r-project.org). In particular, inspection of the MCMC draws used the package CODA (Convergence Diagnostics and Output Analysis; Best *et al.*, 1997).

Application

Before analysing the real dataset, the properties of the model and the performance of the MCMC algorithm were studied on simulated data. Two types of dataset were generated according to the model equations [except for annual recruitment, which did not follow Equation (1), but were instead taken as the estimated values from the SICA model, as explained below], emulating the main features of the real data. Datasets of the first type corresponded to the years 1987–2004. Although the real dataset analysed here runs until 2008, given the fishery closures since 2005, it was easier to simulate realistic datasets terminating the simulated dataseries in 2004. For each dataset of the first type, a second one was considered, which was identical to the first until 1999, but incorporated a fishery closure from year 2000. Population levels differed from the first dataset only since year 2000, owing to the absence of fishing, and new survey observations were simulated for those years. Observations on growth rates at age were the same as in the first dataset. The purpose of the second type of dataset was to explore whether the absence of catches allowed better estimation of the rates of natural mortality. For each type of dataset, 15 replicates were generated, all 15 corresponding to the same underlying population values and parameters in the observation equations, differing only in the actual observed data.

The results presented here are based on MCMC runs with random starting values sampled from the prior distributions. Mixing of the chains was slow because of high correlation between the parameters. Chain behaviour was examined by visually inspecting traces, cumulative plots, and autocorrelation functions. Convergence diagnostics implemented in CODA confirmed that chain length (1 100 000 iterations), burn-in period (first 100 000 iterations discarded), and thinning interval (1 out of 200 iterations kept) were sufficient to estimate the posterior median and 90% probability intervals with the reported accuracy.

Simulated data

Simulated data were based on the results of the SICA model run on data from 1987 to 2004 (ICES, 2005), under the assumption that natural mortality was $M_1 = M_{2+} = 1.2$. SICA was used instead of ICA, because it allows modelling various fleets throughout the year, which is relevant for Bay of Biscay anchovy.

Initial biomass (B_0) and annual recruitment (R_y) were taken to be the values estimated by SICA, after converting numbers into biomass using the stock weights. Annual fishing mortality rates by semester, $f(\text{sem}_j, y)$, were also computed from the SICA estimates as the average of the rates of fishing mortality of each of the fisheries within each semester (the winter French fishery, the Spanish and French spring fisheries for the first semester, and the Spanish and French fisheries for the second semester). Similarly, age 1 selectivity was taken as the average of age 1 selectivity SICA estimates of the fisheries in each semester, resulting in $s(\text{sem}_1,1) = 0.318$ and $s(\text{sem}_2,1) = 0.824$. The selectivity of the 2+ age class was fixed at 1, as already mentioned. Intrinsic growth parameters were calculated as the average log ratio of the stock weights-at-age, leading to $G_1 = 0.6$ and $G_{2+} = 0.2$. Total population biomass and age 1 proportion at survey time and total catch biomass and age 1 proportion in each semester were calculated from the above parameters values using Equations (3)–(10).

Catchability values of the DEPM and acoustic survey indices from SICA were used ($q_{\text{depm}} = 1$, $q_{\text{ac}} = 1.35$). The other parameters in the observation equations were taken as $\psi_{\text{depm}} = 35$, $\psi_{\text{ac}} = 70$, and $\xi_{\text{depm}} = \xi_{\text{ac}} = 4.68$, derived from the estimated standard errors of the real survey indices until 2008. The precision of the observation equation of total catch was taken as $\psi_{\text{catch}} = 400$, which corresponds to a *CV* of ~5%. This is considered a realistic *CV* for anchovy catches, because experts consider that the quantity caught is known essentially without error. The parameter affecting the variance of the observed age proportion in the catch was taken as $\xi_{\text{catch}} = 4$, leading to a smaller precision of the observed age proportion for the catch than for the surveys. The precision of the observation equation of the growth-rate parameters was taken as $\psi_G = 36$ based on the precision of the observations in the real dataset. Total biomass indices, age 1 biomass proportion estimates, observed total catch by semester, observed age 1 biomass proportion in the catch, and observed intrinsic growth rates by age were drawn from observation equations (11)–(15), conditioning on the "true" population and values of the parameters intervening in the equations.

Four different inference settings were explored, depending on whether the DEPM survey was assumed to provide an absolute or a relative abundance index ($q_{\text{depm}} = 1$ or estimated) and on whether the rates of natural mortality by age were assumed known or unknown ($M_1 = M_{2+} = 1.2$ or estimated). Table 2 summarizes posterior inference on model parameters for one replicate dataset of the first type (i.e. with data from 1987 to 2004, without fishery closure). Most of the general features of the results are, however, representative of the results found for other replicate datasets of the same type. Under the four settings, the "true"

Table 2. Results for the first type of simulated dataset (1987–2004, without fishery closure), for different assumptions on natural mortality and DEPM survey catchability, listing posterior quantiles for a particular replicate and the median across all replicates of the individual posterior medians.

		DEPM absolute								**DEPM relative**							
		M_1 and M_{2+} estimated				**M_1 and M_{2+} fixed**				**M_1 and M_{2+} estimated**				**M_1 and M_{2+} fixed**			
		1 replicate			**All**	**1 replicate**			**All**	**1 replicate**			**All**	**1 replicate**			**All**
Parameter	**"True"**	**5%**	**50%**	**95%**	**50%**	**5%**	**50%**	**95%**	**50%**	**5%**	**50%**	**95%**	**50%**	**5%**	**50%**	**95%**	**50%**
q_{depm}	1	–	–	–	–	–	–	–	–	0.72	0.92	1.10	1.02	0.89	1.01	1.14	1.01
q_{ac}	1.35	1.23	1.33	1.44	1.34	1.24	1.34	1.45	1.34	0.96	1.22	1.47	1.32	1.18	1.35	1.51	1.31
ψ_{depm}	35	21.87	41.44	73.54	33.90	22.84	42.50	74.35	31.58	22.12	42.81	75.25	33.35	21.94	41.40	73.78	31.56
ψ_{ac}	70	26.39	54.61	105.31	55.25	26.65	53.57	102.21	54.41	28.55	56.96	108.20	56.96	26.49	52.86	98.89	53.63
ξ_{depm}	4.68	3.61	4.33	5.03	4.68	3.73	4.37	5.02	4.61	3.59	4.29	4.91	4.71	3.72	4.41	5.03	4.64
ξ_{ac}	4.68	4.31	5.19	6.29	4.52	4.43	5.14	5.97	4.60	4.42	5.20	6.22	4.53	4.38	5.17	6.15	4.59
ξ_{catch}	4	3.19	3.63	4.04	4.03	3.22	3.66	4.06	3.99	3.21	3.64	4.03	4.00	3.17	3.64	4.03	3.98
B_0	28 000	24 343	29 437	35 954	27 447	23 389	27 447	32 209	26 108	24 588	31 571	41 773	28 283	22 925	27 447	33 190	26 635
μ_R	–	10.35	10.68	10.99	10.68	10.42	10.72	11.03	10.68	10.42	10.79	11.19	10.69	10.39	10.72	11.03	10.69
ψ_R	–	1.02	1.80	2.86	1.69	1.00	1.78	2.88	1.69	1.00	1.76	2.84	1.69	1.01	1.78	2.84	1.69
$s(\mathrm{sem}_1, 1)$	0.318	0.29	0.34	0.40	0.34	0.29	0.33	0.38	0.33	0.28	0.33	0.39	0.33	0.29	0.33	0.38	0.33
$s(\mathrm{sem}_2, 1)$	0.824	0.56	0.73	0.96	0.76	0.72	0.84	0.99	0.82	0.59	0.77	0.99	0.77	0.72	0.85	0.99	0.83
M_1	1.2	0.75	1.07	1.36	1.14	–	–	–	–	0.84	1.16	1.44	1.15	–	–	–	–
M_{2+}	1.2	1.12	1.40	1.74	1.25	–	–	–	–	1.12	1.37	1.71	1.26	–	–	–	–
G_1	0.6	0.55	0.61	0.67	0.63	0.54	0.60	0.65	0.63	0.55	0.61	0.67	0.63	0.54	0.60	0.66	0.63
G_{2+}	0.2	0.17	0.23	0.29	0.22	0.16	0.21	0.26	0.21	0.17	0.23	0.29	0.21	0.15	0.21	0.27	0.21
ψ_G	36	27.28	41.12	59.00	30.43	27.56	41.23	59.00	30.05	27.17	41.06	59.25	30.19	27.44	41.15	59.12	30.25

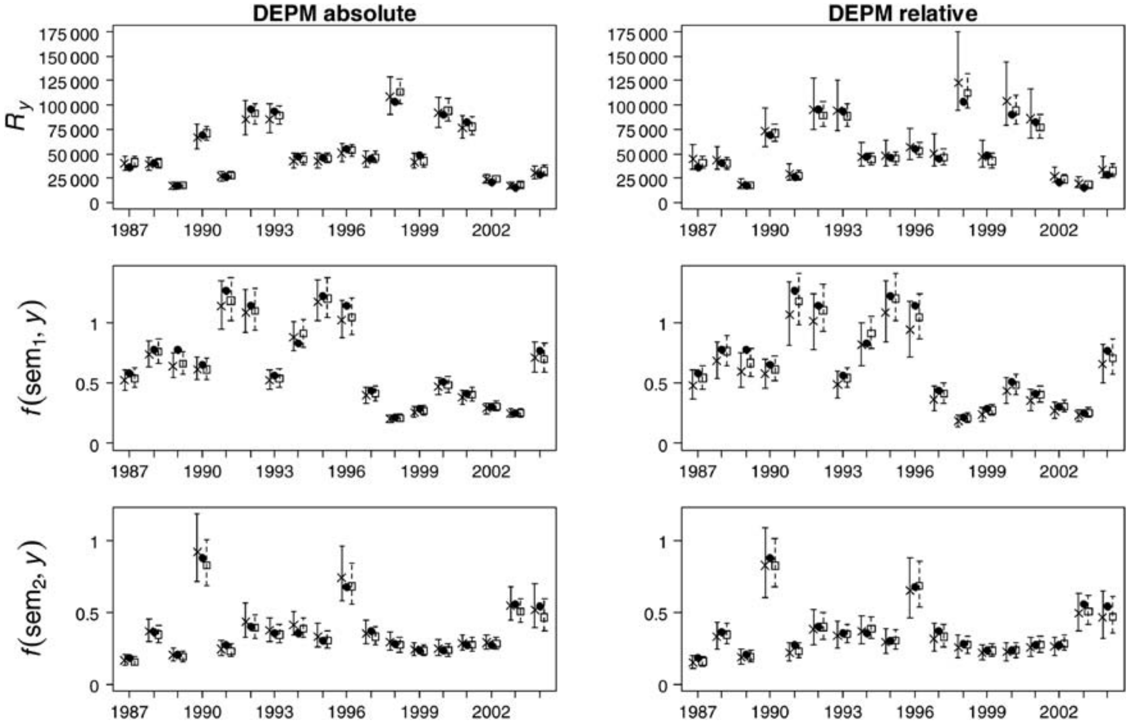

Figure 1. Results for one replicate dataset of the first type. Posterior median and 90% probability intervals of recruitment (top), fishing mortality in the first (middle) and the second (bottom) semesters for different assumptions on natural mortality (solid line and cross when natural mortality is estimated, dashed line and open square when natural mortality is fixed at its "true" value). The black dots represent the "true" values. Left and right panels correspond to DEPM taken as absolute and relative, respectively.

values are within the 90% posterior probability intervals. There are no "true" values for μ_R or ψ_R because annual recruitment was not simulated from Equation (1). Time-series of posterior medians and 90% probability intervals of recruitment and fishing mortalities by semester for the same replicate dataset are compared with "true" values in Figure 1. Clearly, the width of the posterior distribution increases as more parameters are treated as unknown. When natural mortality is considered unknown, the estimates differ by age class, being around 1.1 for recruits and 1.4 for older fish (Table 2). Still focusing on the case of unknown natural mortality, Figure 1 shows that recruitment estimates are slightly larger and fishing mortalities slightly smaller when the DEPM index is taken as relative instead of absolute, a finding which must be related to the lower catchability estimates then obtained. In contrast, when the rates of natural mortality are fixed at their "true" values, posterior quantiles of recruitment and fishing mortality are almost equal regardless of whether the DEPM index is considered absolute or relative. Some of these effects reflect the high posterior correlation between some of the parameters, especially when all of them are estimated (Figure 2). The catchabilities of the two surveys are strongly positively correlated, which is almost certainly related to the very strong negative correlation that they both display with the initial population biomass (B_0) and the average log-recruitment level (μ_R). The catchabilities are also correlated, though less strongly, with the annual fishing mortalities by semester (positively) and with the natural mortality rates (negatively). The rates of natural mortality are very strongly negatively correlated between the two age classes, and also show very strong correlation with age 1 selectivity parameters. The fact that observation equations exist for growth rates directly makes these parameters almost independent of the rest.

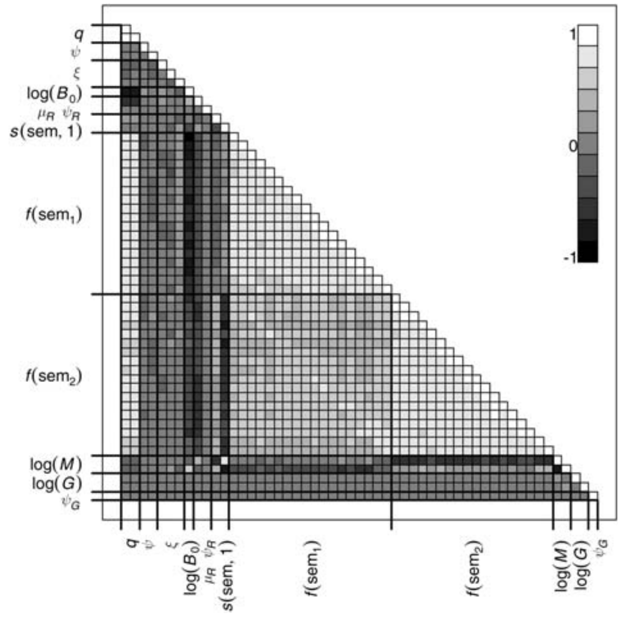

Figure 2. Results for one replicate dataset of the first type. Posterior correlations when all parameters are estimated.

Although, for a particular replicate dataset, the model parameters might be under- or overestimated, when medians

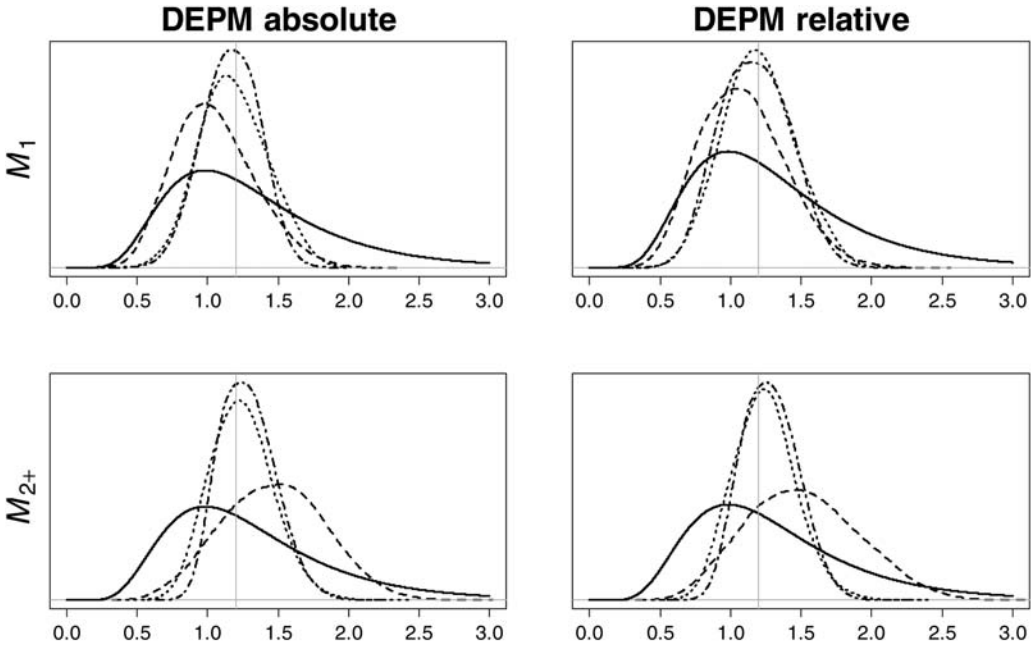

Figure 3. Results for simulated data with and without a fishery closure. Prior (solid line) and posterior density functions of M_1 (first row) and M_{2+} (bottom row), averaged across all replicate datasets. Whole year range (18 years) without fishery closure (dotted line) and with fishery closure (dot dashed line); short year range (first 13 years; dashed line). The left panels correspond to the case when the DEPM survey index is considered an absolute estimate, and the right ones when it is taken as relative. The grey vertical line represents the "true" values ($M_1 = M_{2+} = 1.2$) used to simulate the datasets. The horizontal grey line is a baseline at $y = 0$.

Table 3. Results (posterior quantiles) for the real dataset, for different assumptions regarding natural mortality and DEPM survey catchability.

	DEPM absolute						**DEPM relative**					
	M_1 and M_2 estimated			**M_1 and M_2 fixed**			**M_1 and M_2 estimated**			**M_1 and M_2 fixed**		
Parameter	**5%**	**50%**	**95%**	**5%**	**50%**	**95%**	**5%**	**50%**	**95%**	**5%**	**50%**	**95%**
q_{depm}	–	–	–	–	–	–	0.867	1.110	1.392	0.651	0.800	0.989
q_{ac}	1.042	1.303	1.640	0.918	1.176	1.478	1.061	1.407	1.852	0.800	1.024	1.322
ψ_{depm}	4.162	7.636	13.131	3.547	6.899	12.240	4.264	7.835	13.321	3.738	6.791	11.880
ψ_{ac}	2.539	5.287	9.612	2.339	4.809	9.131	2.632	5.344	9.984	2.398	5.012	9.417
ξ_{depm}	3.019	3.935	5.246	3.198	4.062	5.227	3.173	3.986	4.795	3.108	3.945	4.926
ξ_{ac}	2.628	3.582	4.555	2.640	3.448	4.211	2.799	3.698	4.643	2.550	3.444	4.295
ξ_{catch}	2.573	3.058	3.592	2.466	2.978	3.482	2.584	3.043	3.489	2.514	2.979	3.491
B_0	15 138	20 313	26 370	17 396	23 156	29 733	14 530	18 977	25 349	18 639	25 336	33 523
μ_R	9.879	10.280	10.650	10.110	10.480	10.850	9.775	10.200	10.630	10.220	10.600	10.970
ψ_R	0.619	1.053	1.667	0.595	1.009	1.611	0.610	1.037	1.639	0.609	1.031	1.657
$s(\text{sem}_1, 1)$	0.454	0.560	0.689	0.420	0.509	0.610	0.458	0.566	0.699	0.412	0.499	0.605
$s(\text{sem}_2, 1)$	1.153	1.606	1.946	1.165	1.488	1.853	1.266	1.628	1.949	1.170	1.477	1.840
M_1	0.515	0.836	1.218	–	–	–	0.493	0.797	1.244	–	–	–
M_{2+}	0.716	0.999	1.340	–	–	–	0.701	0.946	1.288	–	–	–
G_1	0.436	0.556	0.670	0.562	0.677	0.808	0.445	0.558	0.673	0.527	0.637	0.759
G_{2+}	0.101	0.179	0.277	0.191	0.299	0.417	0.098	0.179	0.283	0.161	0.253	0.373
ψ_G	11.330	19.000	29.861	7.978	14.320	24.041	11.250	19.055	30.391	9.180	16.485	26.821

of the 5th, 50th, and 95th percentiles are computed across the 15 replicates, the resulting intervals are mostly well centred at the "true" values, and the differences attributable to different assumptions regarding survey catchability and natural mortality rates are also lower. As an illustration, Table 2 displays the median across the 15 replicates of the individual posterior medians.

Datasets of the second type, derived from datasets of the first type but incorporating a fishery closure in the final 5 years, aim to examine whether estimation of natural mortality improves with fishery closure. Figure 3 compares the posterior density functions of M_1 and M_{2+}, averaged across all replicate datasets, using a short year-span (the first 13 years of data) and the whole range of years (18 years), with and without fishery closure in the final

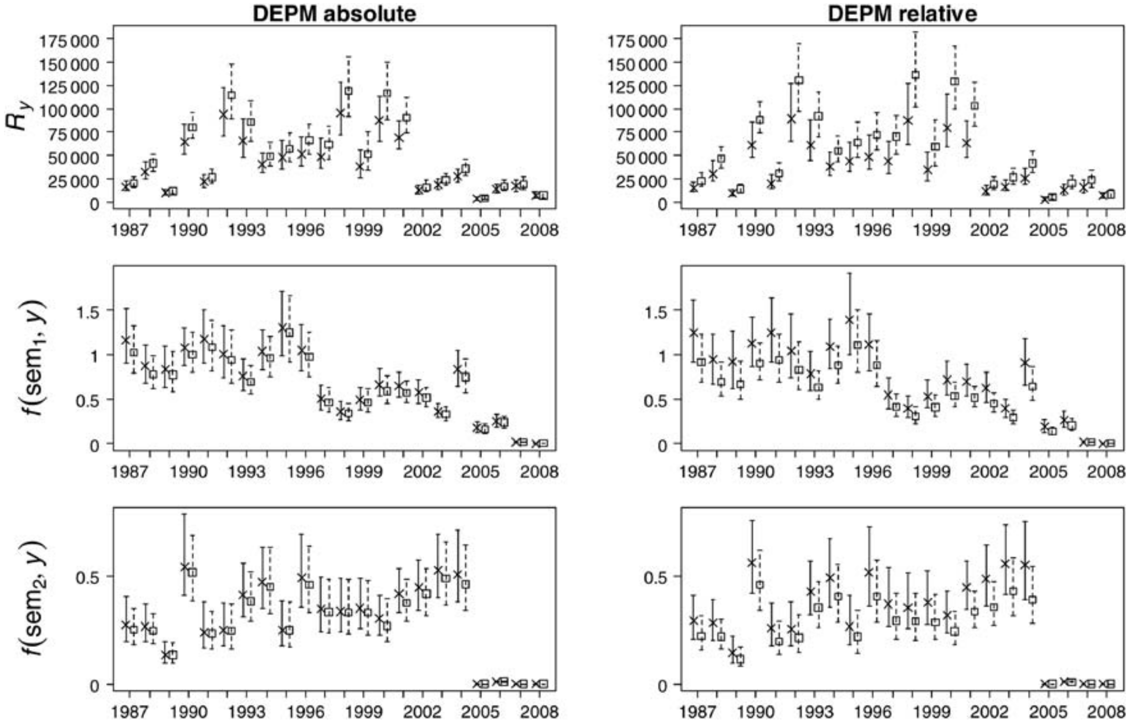

Figure 4. Results for real data. Posterior median and 90% probability intervals of recruitment (top), fishing mortality in the first (middle) and the second (bottom) semesters for different assumptions on natural mortality (solid line and cross when natural mortality is estimated, dashed line and open square when natural mortality is fixed at 1.2). Left and right panels correspond to the DEPM survey index taken as absolute and relative, respectively.

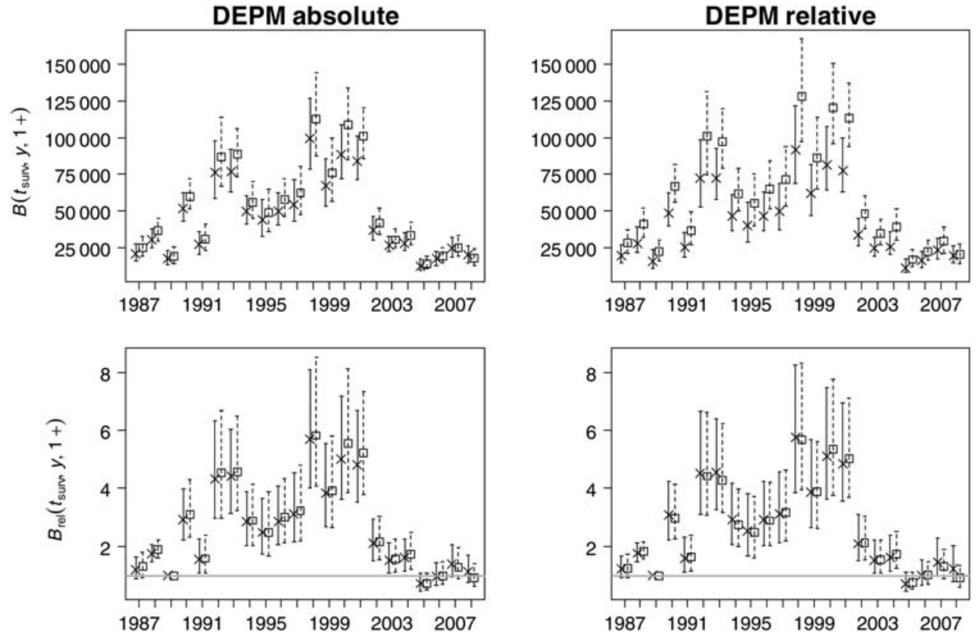

Figure 5. Results for real data. From top to bottom, posterior distributions of the total biomass and of relative biomass at the time of the survey (total biomass at the time of the survey with respect to 1989) for different assumptions on natural mortality (solid line and cross when natural mortality is estimated, dashed line and open square when natural mortality is fixed at 1.2). Left and right panels correspond to DEPM taken as absolute and relative, respectively. The horizontal grey line for the relative biomass represents the 1:1 ratio.

5 years. The left and right panels of the figure correspond to the DEPM survey assumed to be an absolute or a relative abundance index, respectively. When the model was applied to the shorter year-span, M_1 and M_{2+} tended to be under- and overestimated, respectively, independently of the catchability assumption of the DEPM survey. This situation was rectified when the whole range

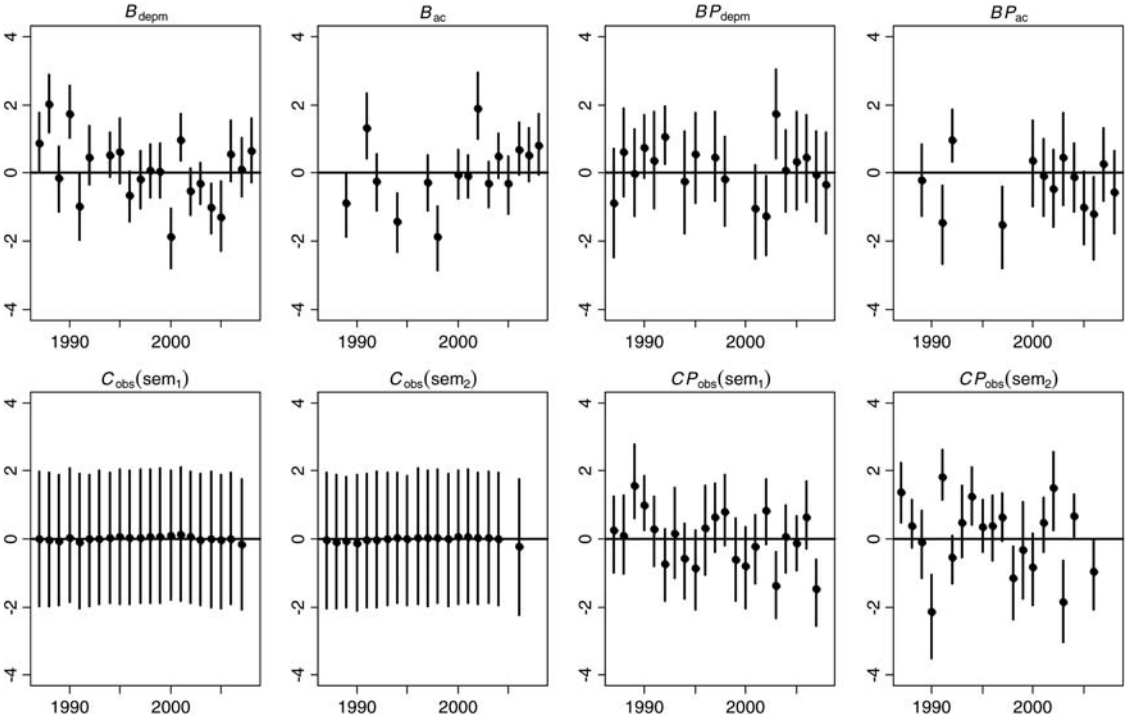

Figure 6. Results for real data. Posterior median (black dot) and 95% probability intervals (vertical segment) of Pearson's residuals of each of the observed time-series when the rates of natural mortality by age are estimated and the DEPM index is considered as absolute. The horizontal solid line is located at zero.

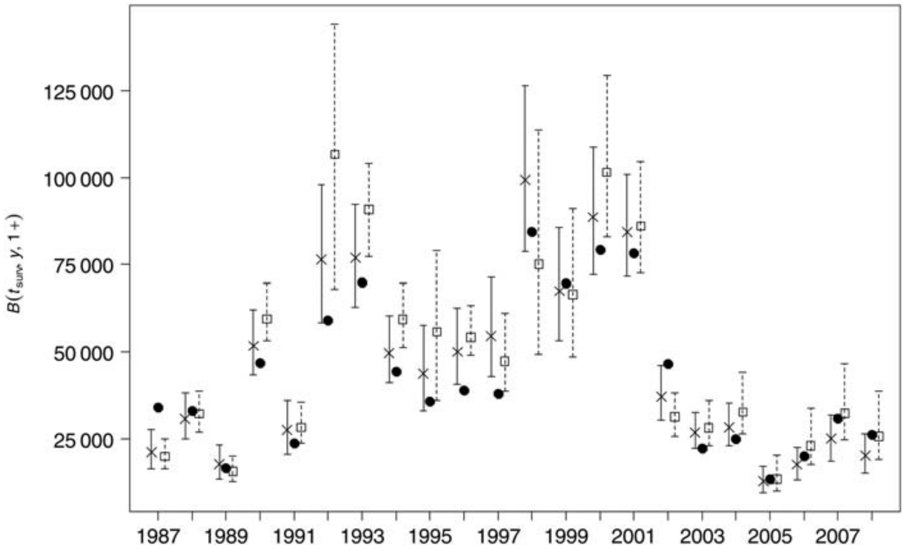

Figure 7. Results for real data. Comparison of the posterior median and 90% probability intervals of total biomass at the time of the survey resulting from the model presented here (solid line and cross) and from the model in Ibaibarriaga *et al.* (2008; dashed line and open square). The bullets correspond to the results from SICA.

of years was considered. In that case, the width of the posterior distributions was also reduced because of the increase in the number of observations. There were almost no differences in the posterior distributions of M_1 and M_{2+} whether the fishery was open or closed. This might be explained by the fact that, in the model developed here, commercial catch observations also provide information on underlying population abundance and model parameters, including rates of natural mortality [see Equations (8)–(10), (13), and (14), noticing that Equation (8) involves population abundances and model parameters].

Real data

The same model settings ($q_{\text{depm}} = 1$ or estimated; $M_1 = M_{2+} = 1.2$ or estimated) were applied to the real dataset for the years

1987–2008 (Supplementary Table S1). Table 3 and Figure 4 show posterior medians and 90% probability intervals for the model parameters and annual recruitment. The biggest differences depend on the natural mortality assumption. When all parameters are estimated, M_1 and M_{2+} are estimated at ∼0.8 and 1, respectively, resulting in greater catchability, lower recruitment, and larger estimates of fishing mortality than when the rates of natural mortality are fixed at 1.2. The top panels of Figure 5 also show the sensitivity of population total biomass estimates at the time of the survey to the assumptions on natural mortality and survey catchability. However, relative biomass, defined as the total biomass at the time of the survey divided by the corresponding quantity in 1989, which is currently used as the reference for management, is almost independent of the assumptions on natural mortality and survey catchability (Figure 5, bottom panels).

Posterior distributions of Pearson's residuals when the DEPM survey index is taken as absolute and M_1 and M_{2+} are estimated are shown in Figure 6. There is no clear pattern in the residuals, so the model seems to be encapsulating the available data. Notably, the residuals of the total catch by semester are close to the desired distribution, centred at zero and with 95% probability intervals between -2 and 2, owing to the high precision imposed on their observation equations.

The results of the model developed here are compared with the results of the previous model (Ibaibarriaga *et al.*, 2008) for the case where the DEPM biomass is taken as absolute, and the rates of natural mortality and growth are estimated. For the parameters common to both models, the prior distributions specified in Table 1 were used. The trends in the posterior median of population biomass are similar for both models, and in most years, the posterior medians obtained from the previous model are within the 90% probability intervals obtained from the new model (Figure 7). The biggest discrepancies are in 1992, 1998, and in the most recent years when the fishery collapsed. In terms of precision, the posterior distributions of the biomass in the recent years when exploitation was very low or zero are narrower in the new model. The trends estimated from the SICA model under the same assumptions ($q_{\text{depm}} = 1$ and M_1 and M_{2+} estimated) are similar (Figure 7). However, even if the SICA biomass estimates are almost always within the posterior 90% probability intervals of the model developed here, they tend to be lower than the posterior medians and close to the fifth percentile. In the final 3 years, this pattern changes, and the SICA biomass estimates are larger than the posterior medians and close to the biomass estimates from the model of Ibaibarriaga *et al.* (2008).

Discussion

Our model is an extension of the model described in Ibaibarriaga *et al.* (2008). It follows the same principles: the population dynamics are described in terms of biomass, with the population divided into two age classes (recruits and older fish), which seems to be sufficient to track the main dynamics of the stock. The model is cast in a Bayesian state-space framework, although the process error is only incorporated in the recruitment process. The main difference is the way in which catch is incorporated. In the previous model, catches were just considered as instantaneous removals from the population. This had the effect of imposing lower bounds on population biomass, particularly on the estimates of annual recruitment. In the present model, fishing is considered to be a continuous process separable into age and year effects, and observed total catch and observed age 1 biomass proportion in the catch are incorporated through observation equations in each semester. In addition, intrinsic growth and natural mortality, which previously were encapsulated by a single parameter, are now disaggregated by process and age class. Incorporating observation equations based on the average weight-at-age of the stock allows precise estimation of the growth rates, and inference on the rates of natural mortality can then be analysed in detail.

Results from simulated datasets showed good model performance, being less sensitive to survey catchability and natural mortality assumptions than the earlier model. Estimated recruitment levels are of the same order of magnitude whether parameters are estimated or fixed, suggesting that, in general terms, incorporating stochastic observation equations for catch helps in determining the population state.

It has been argued that very low exploitation levels or an absence of catches could help estimating the rates of natural mortality. For instance, Sinclair (2001) obtained estimates of natural mortality for cod (*Gadus morhua*) in the southern Gulf of St Lawrence after the fishery closed in 1993. For anchovy, when applying the model to simulated data before (shorter year span) and after (whole year range) a fishery closure, the spread of the posterior distribution was reduced for the longer time-series, and the median of the posterior distribution tended to be closer to the "true" value. However, the same effect was noticed when considering the whole year range without fishery closure. In other words, with the model developed here, improvement in estimating natural mortality comes from having a longer time-series and not from the fishery closure. The reason is that the stochastic observation equations for commercial catch link the observed catch to underlying model abundance and the population parameters, including natural mortality.

Estimates of natural mortality from an application to real data give higher rates of natural mortality for older fish. Similar patterns of recruits growing faster ($G_1 > G_{2+}$) and having lower natural mortality ($M_1 < M_{2+}$) are also found in ICES (2009b) for the same anchovy population. Hence, the assumption of a single parameter jointly accounting for growth and natural mortality and constant across ages seems to be an oversimplification. Estimating different rates of natural mortality for each age is possible under the assumption that survey catchabilities are the same for all ages. ICES (2009b) explored different options, either fixing survey catchabilities while estimating natural mortality rates at age, or estimating survey catchabilities at age while fixing the rates of natural mortality. Trying to estimate all parameters could lead to additional confounding (Cotter *et al.*, 2004, and references therein). Other sources or information from other stocks could be incorporated into a meta-analysis type of approach (Hilborn and Liermann, 1998; McCarthy *et al.*, 2008) to aid in the estimation of natural mortality.

One important aspect of the assessment model used is the information it provides for management advice. With the previous model (Ibaibarriaga *et al.*, 2008), in which catches were simply subtracted from the population, management advice needed to be given in terms of catch and harvest rates (total catch divided by biomass), whereas the present model allows the use of more-common terminology, such as fishing mortality and selectivity at age. The fishing mortality is separated by semester, which allows better characterization of the fisheries exploiting anchovy. The fishing mortality on the 2+ age class is greater in the first than in the second semester. Moreover, in the first semester, age 1 fish are less exploited than age 2+ fish (age 1 selectivity <1), whereas the opposite happens in the second semester (age 1 selectivity >1). These results are in accord with knowledge of the fishery (Uriarte *et al.*, 1996) and are explored in detail in ICES (2005, 2009b), using the SICA model.

The model developed here has allowed estimation of new parameters related to the anchovy stock and fishery dynamics compared with the simpler model described by Ibaibarriaga *et al.* (2008). However, with increasing model complexity, the number of parameters and the cross-correlation between them increases, demanding more data and longer MCMC runs to obtain accurate estimates. Computation time therefore increases significantly. The model in Ibaibarriaga *et al.* (2008) proved to be good enough to track the dynamics of the anchovy population, so for routine assessment it might be sufficient, whereas more-complex models, such as that presented here, may be used to provide contrast from time to time.

In conclusion, it is worth mentioning that the model can also be used for other short-lived species. On the one hand, its relatively simple age structure (just two age-classes) precludes overparametrization while tracking the main recruitment dynamics (Collie and Sissenwine, 1983; Roel and Butterworth, 2000; Mesnil, 2003; Roel *et al.*, 2009). On the other hand, this type of stock is closely monitored using annual fishery-independent surveys, which provide abundance indices that can be used for tuning (Barange *et al.*, 2009). The Bayesian framework allows directly incorporation of uncertainties in the observations that can be further translated to the calculation of biological risks when managing the stock (Hilborn and Liermann, 1998).

Supplementary material

The real dataset is available as supplementary material at the *ICESJMS* online version of this paper.

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