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A mixed-effects approach to estimating time-varying natural mortality in a statistical catch-at-age model: Application to stock assessments for eastern Georges Bank Atlantic Cod and Georges Bank Yellowtail Flounder

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ABSTRACT

A suite of statistical catch-at-age models with time-varying natural mortality (*M*), selectivity and catchability were fitted to data for eastern Georges Bank Atlantic Cod (*Gadus morhua*) and Georges Bank Yellowtail Flounder (*Limanda ferruginea*). Time-varying components were modelled as random walks. The models use a mixed-effects framework in which some of the parameters were assumed to arise from shared distributions. Estimated *M* for older individuals of both stocks increased to high levels over recent years. *M* for younger individuals was difficult to estimate, since these values were highly correlated with recruitment. Estimating time-varying selectivity or catchability did not improve model performance. The increases in *M* estimated by these models are consistent with trends in *M* for other large-bodied groundfish in the northwest Atlantic.

RÉSUMÉ

1. INTRODUCTION

Stock assessment models typically assume that underlying population processes are stationary; however, stock assessment models increasingly show that fundamental recruitment and natural mortality processes can vary widely over time, presumably in response to physical and biological influences. For instance, natural mortality (*M*) for large individuals of several northwest Atlantic groundfish stocks has risen to very high levels over recent years (e.g. Swain and Mohn 2012, Swain and Benoît 2015, Cadigan 2015). Models that assume stationarity in parameters such as *M* typically fail to fit data generated by nonstationary processes and ultimately overestimate the stochasticity associated with the system (Turchin 2003).

Including time-varying parameters in stock assessment models is one way to assess the degree to which suspected non-stationary process may affect management advice. This approach is more or less effective depending on the quality of stock assessment data, population dynamics of the fish species, and the level of information contained in the historical fishing mortality time-series.

This paper presents a statistical catch-at-age model for northwest Atlantic groundfish that attempts to estimate time-varying parameters such as *M*, selectivity, catchability, and recruitment. The model was fitted to data for eastern Georges Bank Atlantic Cod (*Gadus morhua*; eGB cod) and Georges Bank Yellowtail Flounder (*Limanda ferruginea*; GB Yellowtail Flounder). Existing assessment models for both of these stocks assume stationary parameters and both assessments show strong retrospective patterns in biomass, fishing mortality, and recruitment estimates (Legault et al. 2014, Andrushchenko et al. 2016), which suggests that underlying population processes may be varying over time.

2. METHODS

2.1 STATISTICAL CATCH-AT-AGE MODEL

We developed a statistical catch-at-age (SCA) model that estimates trends in abundance and mortality by fitting to commercial fishery catch-at-age along with indices of abundance and age-composition data from three bottom trawl surveys that are conducted annually on Georges Bank (the DFO survey, the NMFS spring survey and the NMFS fall survey). Temporal trends in natural mortality, selectivity and catchability are estimated by modelling those processes as random walks. This approach has become increasingly popular for modelling changes in population processes for other species (Fu and Quinn 2000, Jiao et al. 2012, Swain et al. 2015). Below we provide several alternative structural forms of the model by incorporating age blocks used for M as well as alternative forms of fishery and survey age selectivity.

The model uses a mixed-effects framework in which some parameters, termed “random effects” (collectively denoted as Θ^{rand}) are assumed to arise from a shared distribution. All other freely estimated parameters (collectively denoted as Θ^{est}) are termed “fixed-effects”.

Model parameters are partitioned into three subsets consisting of fixed-effects parameters (Θ^{est}), conditionally estimated parameters (Θ^{cond}), including catchability and variance parameters estimated conditionally on the other parameters, and random-effects parameters (Θ^{rand}) representing process errors in time-varying parameters, including, where applicable, *M*, recruitment, selectivity, and catchability.

The sections below describe components of the model, which we implemented using the Template Model Builder package (TMB; Kristensen et al. 2016) within R (R Core Team 2016). Model notation and equations are given in Table 1 and Table 2, respectively. Likelihood equations are given in Table 3. Model equations are labelled with “M” with likelihood equations are labelled with “L” (e.g. equation M.1 or L.1).

2.2 SELECTIVITY

Selectivity-at-age is parameterized either as an asymptotic (logistic function) or dome-shaped (Normal pdf) function of age (M.6). Asymptotic selectivity is parameterized using age-at-50% selectivity ($S_{50,g}$) and at-at-95% selectivity ($S_{95,g}$), while dome-shaped selectivity is based on a fully selected age class ($S_{\max,g}$) and a variance parameter ($\sigma^2_{\max,g}$). We allow for selectivity to vary over time as a random walk (i.e., the value of $S_{50,g}$ in a given year is equal to the value from the previous year plus a random deviation) with freely estimated variance ($\sigma^2_{S,g}$) (M.4-M.5). Alternatively, we modeled constant selectivity by fixing $\sigma^2_{S,g}$ at 0.

2.3 MORTALITY

Natural mortality is modeled separately for groups of consecutive ages, termed “age blocks”. Age blocks can be defined based on life history traits (i.e., a juvenile block and an adult block) or to facilitate the investigation of a particular hypothesis (i.e., predation on a specific age class).

We model two age blocks. The first age block (b_1) contains younger fish (ages 1-5 for eGB cod and age 1-2 for GB Yellowtail Flounder) while the second age block (b_2) contains older fish (ages 6+ for eGB cod and ages 3+ for GB Yellowtail Flounder). Natural mortality in the older age block always varies as a random walk. Allowing natural mortality in the younger age block to vary is more challenging, as juvenile natural mortality is strongly correlated with recruitment, so we compare three parameterizations of *M* for the younger age block: (i) *M* fixed at 0.25 yr^{-1}, (ii) *M* estimated, but constant over time, (iii) *M* estimated as a random walk.

We iteratively solve the Baranov catch equation (M.15) to obtain the fully selected fishing mortality for the commercial fishery (F_t). Fishing mortality-at-age is then obtained by multiplying F_t by selectivity-at-age in the commercial fishery (M.9).

2.4 STATE DYNAMICS

Recruitment is the product of the mean recruitment rate (r) and an annual deviation ($\varepsilon_{R,t}$), which is assumed to normally distributed with zero mean and variance $\sigma^2_{R,t}$ (M.11). The mean recruitment rate and variance are both freely estimated. Numbers-at-age (except recruits) in the first model year are also freely estimated (M.12).

Cohorts are propagated through the model on an annual time step (M.13). The maximum age class *A* is modeled as a plus group.

2.5 OBSERVATION MODELS

Biomass index observations consist of catch rate observations for GB Yellowtail and estimates of age 1+ biomass for eGB Cod. We modeled each of the biomass indices assuming that the index is obtained after some fraction d_g of year has expired. We model catchability ($q_{g,t}$) as a random walk in time, where annual deviations ($\varepsilon_{q,t}$) are assumed to have zero mean and variance $\sigma^2_{q,g}$ where q indicates a catchability variance and g indexes the source (M.16). Alternatively, we modeled constant catchability by fixing $\sigma^2_{q,g}$ at 0.

Information about changes in population age-structure consists of catch-at-age data from the commercial fisheries and three bottom trawl surveys. We converted catch-at-age to proportions-at-age and assumed no ageing error.

2.6 OBJECTIVE FUNCTION

The objective function for this model consists of likelihood functions for observations and random effects (Table 3).

Biomass index observations are assumed to be log-normally distributed with mean given by M.17 and variance $\tau^2_{I,g}$ where I indicates a biomass index variance and g indexes the source. The residual function in L.1 is used in computing the conditional MLE for log-catchability in L.2 and sum-of-squares in L.3. The conditional MLE for $\tau^2_{I,g}$ is given in L.4 and the concentrated likelihood in L.5 (Bard 1978). Data sources influence the estimation procedure via their estimated variances; no arbitrary weighting factors are used to adjust the influence of alternative data sources.

The age-composition data are modelled using a multivariate-logistic (MVL) distribution on the proportions-at-age (Schnute and Richards 1995, Schnute and Haigh 2007). Equation L.6 gives the residual function, L.7 the sum-of-squares, and L.8 the conditional MLE for the variance $\tau^2_{P,g}$ where P indicates an age-composition variance and g indexes the source. The MVL distribution has at least two advantages over the more traditional multinomial distribution for age composition. First, it is more realistic to treat an age-composition sample as *A* (number of age classes, e.g., 8), potentially noisy, observations rather than *N* (number of samples, e.g., 600) independent samples. Second, the variance is determined by the fit rather than the sample size, *A*, so re-weighting the age composition data via some complicated iterative scheme is unnecessary. In addition, the biomass index and age composition variances are comparable.

All random effects are assumed to be normally distributed with zero mean and freely estimated variance parameters. (L.10-L.13).

The negative joint log-likelihood of the data and the random effects is the sum of the seven likelihood components (L.15). Fixed effects (Θ^{est}) are estimated by maximizing

$$L\left(\Theta^{est}\right)=\int \exp\left(-f\left(\Theta^{rand},\Theta^{est}\right)\right)d\Theta^{rand}$$

with respect to Θ^{est}, where $L\left(\Theta^{est}\right)$ is the marginal distribution obtained by integrating the random effects out of the joint likelihood. TMB was used numerically approximate $L\left(\Theta^{est}\right)$ via

the Laplace approximation and to evaluate the gradient function for $L\left(\Theta^{est}\right)$. Maximum likelihood estimates of the model parameters were obtained using the nlminb function in R.

2.7 MODEL SCENARIOS

Natural mortality, selectivity and catchability all have multiple possible parameterizations (Table 4). Each combination of parameterizations represents a unique model, which is named by combining the labels listed in Table 4. For example, a model named “mFix-qRW-sCon-cAAAA” will feature (i) fixed, time-invariant natural mortality for ages 1-5, (ii) time-varying catchability, (iii) time-invariant selectivity, and (iv) asymptotic selectivity for each fishery. We fit all possible models (n=196) to both eGB cod and GB yellowtail datasets and discarded models which produced biologically unrealistic estimates. We ranked the remaining models using AIC (Akaike 1974).

3. EASTERN GEORGES BANK ATLANTIC COD

For eGB cod, we fit the SCA to commercial fishery catch-at-age (ages 1-8+, 1978-2015) along with indices of abundance and age composition data from the DFO survey (ages 1-8+, 1986-2015), the NMFS spring survey (ages 1-8+, 1978-2015) and the NMFS fall survey (ages 1-8+, 1978-2015). Separate age blocks for ages 1-5 and ages 6+ were used. Catchability for the NMFS spring survey was estimated separately for the periods 1978-1981 and 1982-2012 to reflect a change in gear in 1982.

3.1 RESULTS

The top-ranked models are listed in Table 5 and their output and diagnostics are displayed in Figures 3-17. All models not listed in Table 5 either produced biologically implausible results, fit the data poorly or were not parsimonious.

Models assuming constant catchability and constant selectivity were selected as the best models (Table 5). When time-varying catchability or time-varying selectivity was assumed, associated variances were estimated to be extremely small values, indicating that either no temporal trend was evident in those processes or that those models were overparameterized.

All models showed large increases in *M* for ages 6+. In particular, the top ranked models estimated that *M* for ages 6+ increased from around 0.25 yr^{-1} in 1978 to ~1.5 yr^{-1} in recent years.

Both top-ranked models assumed that catchability, selectivity and *M* for ages 1-5 were time-invariant, and that selectivity for all surveys except NMFS fall were asymptotic. The models only differed in their treatment of time-invariant *M* for ages 1-5, which the first-ranked model treated as estimable (M=0.37 yr^{-1}) and which the second-ranked model treated as fixed (M=0.25 yr^{-1}). This difference in *M* produced very different model output as the model with higher *M* needs more recruits to compensate for its high mortality. For instance, mean recruitment in the first-ranked model is twice as high as in the second-ranked model.

In general, models were highly dependent on the parameterization of *M* for ages 1-5 as well as prior values. Varying *M* for ages 1-5 as a random walk produced implausibly high values of both *M* and recruitment. Treating *M* for ages 1-5 as time-invariant produced better fits to the data and more realistic model output compared to time-varying *M*; however, even estimating a single time-invariant *M* value is potentially problematic, as this value is only constrained by its prior distribution. Hence, the best approach may be the fix *M* for younger ages.

All of the top-ranked models tracked the survey indices reasonably well given the noise in the data. Conversely, model fits to the age data were very poor, particular for the NMFS spring and NMFS fall surveys, which produced residual standard errors around 1. Retrospective patterns were acceptable for all top-ranked models.

4. GEORGES BANK YELLOWTAIL FLOUNDER

For GB Yellowtail Flounder, we fit the SCA described in section 2 to commercial fishery catch-at-age (ages 1-6+, 1973-2015) along with indices of abundance and age composition data from the DFO survey (ages 1- 6+, 1987-2015), the NMFS spring survey (ages 1-6+, 1973-2015) and the NMFS fall survey (ages 1-6+, 1973-2015). We used separate age blocks for ages 1-2 and ages 3-6+.

4.1 RESULTS

The top-ranked models are listed in Table 6 and their output and diagnostics are displayed in Figures 18-26. All models not listed in Table 6 either produced biologically implausible results, fit the data poorly or were not parsimonious.

Estimated fishing mortality in the top-ranked models was significantly higher before 1995 ($F \approx 0.95$ yr^{-1}) than after ($F \approx 0.14$ yr^{-1}). While estimated recruitment was strong for 1995-2008, recruitments since then are among the smallest in the time series.

Models assuming constant catchability and constant selectivity were selected as the best models (Table 6). When time-varying catchability or time-varying selectivity were assumed, associated variances were estimated to be extremely small values, indicating that either no temporal trend was evident in those processes or that those models were overparameterized.

All models showed large increases in *M* for ages 3-6+. In particular, the top ranked models estimated that *M* increased from around 0.25 yr^{-1} in 1973 to ~1.0 yr^{-1} in recent years.

As with the eGB cod models in section 3, output from GB Yellowtail Flounder models was highly dependent on the parameterization of *M* for the youngest age block (ages 1-2). Varying *M* for ages 1-2 as a random walk produced implausibly high values of both *M* and recruitment. Unlike the eGB cod models, however, time-invariant *M* for younger ages classes were estimated without much influence from the prior distribution.

Retrospective patterns were minimal for all top ranked models.

5. DISCUSSION

SCA models with time-varying natural mortality appear to remove retrospective patterns in assessments models for both GB Yellowtail Flounder and eGB cod. Retrospective patterns for recruitment and fishing mortality in the top-ranked models were minimal for both stocks; however, there was a retrospective pattern in *M* for ages 6+ associated with a steep rise over recent years.

Increases in *M* for age 6+ eGB cod predicted by the SCA were similar to those detected in VPA with time-varying *M* (Swain 2013), which should strengthen confidence in both models; however, the two models differed in their ability to estimate *M* for ages 1-5. While the VPA estimated a declining trend for *M* for ages 1-5 terminating at less than 0.1 yr^{-1}, the SCA estimated extremely high values of *M* for ages 1-5. This behavior from the SCA model is due to the strong correlation between juvenile *M* and recruitment.

Estimated increases in *M* among older fish for both eGB cod and GB Yellowtail Flounder were dramatic but not unprecedented among large bodied groundfish in the northwest Atlantic. For instance, adult *M* greater that 1.0 yr^{-1} has been detected for southern Gulf of St. Lawrence (sGSL) white hake (*Urophycis tenuis*), eastern Scotian Shelf cod, and northern cod in recent decades (Swain and Mohn 2012, Swain and Benoît 2015, Cadigan 2015).

The causes of elevated *M* among large bodied groundfish in the northwest Atlantic have been studied in most detail for sGSL cod, where unreported catch, emigration, or increased *M* due to predation, disease, contaminants, poor fish condition, life-history change and parasites have all been considered as causes. Among these possible explanatory factors, predation is the hypothesis most strongly supported by the weight of evidence (Swain et al. 2011). The predator driving adult *M* in sGSL cod appears to be grey seals (*Halichoerus grypus*), which have increased dramatically in abundance over recent decades (Swain and Benoît 2015). While the diet of grey seals is difficult to establish due to spatial, seasonal and individual heterogeneities, diet samples of seals taken in the vicinity of overwintering sGSL cod aggregations show high proportions of cod. Moreover, simulations based on the energetic requirements of seals and the spatiotemporal overlap of seals with sGSL cod have demonstrated that grey seals could account for a high proportion of sGSL cod *M*, even if the contribution of cod to the seal diet was modest (Benoît et al. 2011). The degree to which grey seals influence *M* in GB fish is unknown, though satellite tagging has shown high proportions of grey seals foraging on Georges Bank and neighbouring waters in winter and early spring (Breed et al. 2006).

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Table 1. Model notation and parameter values.

Symbol	Value	Description
T		Total number of years
A		Plus group age-class
B		Number of natural mortality age blocks
G	4	Number of fisheries
t	$1,2,\ldots,T$	Annual time step
a	$1,2,\ldots,A$	Age-class index
b	$1,2,\ldots,B$	Age-block index
g	$1,2,\ldots,G$	Fishery index: 1=Commercial fishery, 2=DFO survey, 3=NMFS spring survey, 4=NMFS fall survey
$\widehat{N}_{a,1}$		Initial numbers by age class
r		Mean recruitment
ε_t^r		Recruitment process errors
σ_r^2		Recruitment process error variance
m_b		Initial natural mortality for age block b (yr^{-1})
μ_b		Prior mean for initial natural mortality (yr^{-1})
σ_b^2		Prior variance for initial natural mortality
ε_t^M		Natural mortality process errors
σ_M^2		Natural mortality process error variance
q_g		Catchability for fishery $g=2,3,4$
ε_{gt}^q		Catchability process errors for fishery $g=2,3,4$
σ_{gA}^2		Catchability process error variance for fishery $g=2,3,4$

Symbol	Value	Description
$S_{g,a,t}$		Selectivity-at-age in year t for fishery g
$S_{50,g}, S_{95,g}$		Age-at-50% and -95% selectivity for fishery g
$S_{\max,g}, \sigma^2_{S,g}$		Normal selectivity mode and variance
$\varepsilon^S_{g,t}$		Selectivity process errors for fishery g
$\sigma^2_{S,g}$		Selectivity process error variance for fishery g
$\tau^2_{I,g}$		Biomass index variance for fishery $g = 2,3,4$
$\tau^2_{P,g}$		Age proportion variance for fishery g
$N_{a,t}$		Number of age a fish in year t
$B_{g,t}$		Biomass available to fishery $g = 2,3,4$ in year t
$Z_{a,t}$		Total mortality-at-age in year t (yr^{-1})
$M_{a,t}$		Natural mortality-at-age in year t (yr^{-1})
F_t		Fully selected fishing mortality in year t (yr^{-1})
$w_{a,t}$		Weight-at-age in year t (mt)
d_g	0,0.17,0.28,0.79	Survey date, expressed as Julian date / 365

Table 2. Age-structured model equations defining the population dynamics and observations for either eGB cod or GB Yellowtail Flounder. Parameter subsets in are as follows: Θ^{est} estimated as free parameters, Θ^{cond} estimated conditional on free parameters, and Θ^{rand} estimated as random effects.

Catch-at-age model

Parameters

M.1 $$\Theta^{est} = \begin{cases} \left(\left\{ \widehat{N_{a,1}} \right\}_{a=2:A}, r, \sigma_r^2, \left\{ m_b \right\}_{b=1:B}, \sigma_{q,g}^2, \left\{ \sigma_{M,b}^2 \right\}_{b=1:B}, \left\{ S_{50,g} \right\}_{g=1:G}, \left\{ S_{95,g} \right\}_{g=1:G}, \sigma_{S,g}^2 \right) & \text{asymptotic} \\ \left(\left\{ \widehat{N_{a,1}} \right\}_{a=2:A}, r, \sigma_r^2, \left\{ m_b \right\}_{b=1:B}, \sigma_{q,g}^2, \left\{ \sigma_{M,b}^2 \right\}_{b=1:B}, \left\{ S_{\max,g} \right\}_{g=1:G}, \left\{ \sigma_{\max,g}^2 \right\}_{g=1:G}, \sigma_{S,g}^2 \right) & \text{dome-shaped} \end{cases}$$

M.2 $$\Theta^{cond} = \left(\left\{ q_g \right\}_{g=2:G}, \left\{ \tau_{I,g} \right\}_{g=2:G}, \left\{ \tau_{p,g} \right\}_{g=1:G} \right)$$

M.3 $$\Theta^{rand} = \left(\left\{ \varepsilon_{R,t} \right\}_{t=2:T}, \left\{ \varepsilon_{M,b,t} \right\}_{t=2:T}^{b=1:B}, \left\{ \varepsilon_{q,g,t} \right\}_{t=2:T}^{g=2:G}, \left\{ \varepsilon_{S,g,t} \right\}_{t=2:T}^{g=1:G} \right)$$

Selectivity

M.4 $$S_{50,g,t} = \begin{cases} S_{50,g} & t = 1 \\ S_{50,g,t-1} \exp\left(\varepsilon_{S,g,t} \right) & t > 1 \end{cases} \quad \text{asymptotic}$$

M.5 $$S_{\max,g,t} = \begin{cases} S_{\max,g} & t = 1 \\ S_{\max,g,t-1} \exp\left(\varepsilon_{S,g,t} \right) & t > 1 \end{cases} \quad \text{dome-shaped}$$

M.6 $$S_{g,a,t} \propto \begin{cases} \left(1 + \exp\left[-\log(19) \left(a - S_{50,g,t} \right) / \left(S_{95,g} - S_{50,g,t} \right) \right] \right)^{-1} & \text{asymptotic} \\ \exp\left(\dfrac{-\left(a - S_{\max,g} \right)^2}{\sigma_{\max,g}^2} \right) & \text{dome-shaped} \end{cases}$$

Mortality

M.7 $$M_{a,0} = m_i \quad a \in b_i$$

Catch-at-age model

M.8 $$M_{a,t} = M_{a,t-1}\exp\left(\varepsilon_t^m\right) \quad t > 1$$

M.9 $$F_{a,t} = S_{1,a,t}F_t$$

M.10 $$Z_{a,t} = M_{a,t} + F_{a,t}$$

State dynamics

M.11 $$N_{1,t} = r\exp(\varepsilon_{R,t})$$

M.12 $$N_{a,1} = \widehat{N_{a,1}} \quad a > 1$$

M.13 $$N_{a,t} = \begin{cases} N_{a-1,t-1}e^{-Z_{a-1,t-1}} & a < A, \quad t > 1 \\ N_{a-1,t-1}e^{-Z_{a-1,t-1}} + N_{a,t-1}e^{-Z_{a,t-1}} & a = A, \quad t > 1 \end{cases}$$

M.14 $$B_{g,t} = \sum_a w_{a,t}S_{g,a,t}N_{a,t}\exp\left(-d_g Z_{a,t}\right)$$

M.15 $$C_{a,t} = w_{a,t}N_{a,t}\frac{F_{a,t}}{Z_{a,t}}\left(1-\exp\left(-Z_{a,t}\right)\right)$$

Observation models

M.16 $$q_{g,t} = \begin{cases} q_g & t = 0 \\ q_{g,t}\exp\left(\varepsilon_{q,g,t}\right) & t > 1 \end{cases}$$

M.17 $$\hat{I}_{g,t} = q_{g,t}B_{g,t}$$

M.18 $$\widehat{u_{g,a,t}} = \frac{N_{a,t}S_{g,a,t}e^{-d_g Z_{a,t}}}{\sum_j N_{a,t}S_{g,a,t}e^{-d_g Z_{a,t}}}$$

Table 3. Negative joint log-likelihood of the data and the random effects (f).

Likelihoods and Priors
Observations: Biomass indices
L.1 $z_{g,t} = \log I_{g,t} - \log \hat{I}_{g,t}$
L.2 $\widehat{\log q_g} = \frac{1}{n_{I,g}} \sum_{t=1:n_{I,g}} z_{g,t}$
L.3 $Z_{I,g} = \sum_{t=1:n_{I,g}} \left(z_{g,t} - \widehat{\log q_g} \right)^2$
L.4 $\hat{\tau}^2_{I,g} = \frac{1}{n_{I,g} - 1} Z_{I,g}$
L.5 $\ell_I = \sum_{g=2:G} n_{I,g} \log \hat{\tau}^2_{I,g}$
Observations: Age-composition
L.6 $\eta_{g,a,t} = \log p_{g,a,t} - \log \hat{u}_{g,a,t} - \frac{1}{n_{P,g,t}} \sum_{a=1:n_{P,g,t}} \left[\log p_{g,a,t} - \log \hat{u}_{g,a,t} \right]$
L.7 $Z_{P,g} = \sum_{t=1:T} \sum_{a=1:n_{P,g,t}} \eta^2_{g,a,t}$
L.8 $\hat{\tau}^2_{P,g} = \frac{1}{n_{P,g}} Z_{P,g}$
L.9 $\ell_P = \sum_{g=1:G} n_{P,g,x} \log \hat{\tau}^2_{P,g,x}$
Random effects: recruitment, natural mortality, catchability, selectivity
L.10 $\ell_R = \frac{T-1}{2} \log \sigma^2_R + \frac{1}{2\sigma^2_R} \sum_{t=2:T} \left(\varepsilon_{R,t} \right)^2$
L.11 $\ell_M = \frac{T-1}{2} \sum_b \log \sigma^2_{M,b} + \sum_b \sum_{t=2:T} \frac{\varepsilon^2_{M,b,t}}{2\sigma^2_{M,b}}$

Likelihoods and Priors

L.12 $$\ell_q = \frac{T-1}{2}\sum_g \log\sigma^2_{q,g} + \sum_g \sum_{t=2:T} \frac{\varepsilon^2_{q,g,t}}{2\sigma^2_{q,g}}$$

L.13 $$\ell_S = \frac{T-1}{2}\sum_g \log\sigma^2_{S,g} + \sum_g \sum_{t=2:T} \frac{\varepsilon^2_{S,g,t}}{2\sigma^2_{S,g}}$$

Prior distributions: initial natural mortality

L.14 $$\ell_m = \sum_b \frac{\left(m_b - \mu_b\right)}{2\sigma^2_{m,b}}$$

Negative joint log-likelihood

L.15 $$f = \ell_I + \ell_A + \ell_R + \ell_M + \ell_q + \ell_S + \ell_m$$

Table 4. Model processes with multiple parameterizations. Each model scenario is a combination of one parameterization for each process.

Process	Parameterizations	Label
Natural mortality for age block 1	1) Time-invariant, fixed at 0.25 yr^{-1}	mFix
	2) Time-invariant, estimated	mCon
	3) Random walk in time	mRW
Catchability	1) Time-invariant	qCon
	2) Random walk in time	qRW
Selectivity (stationarity – all fisheries)	1) Time-invariant	sCon
	2) Random walk in time	sRW
Selectivity (curve – commercial/DFO/spring/fall)	1) Asym/Asym/Asym/Asym	cAAAA
	2) Dome/Asym/Asym/Asym	cDAAA
	3) Asym/Dome/Asym/Asym	cADAA
	4) Dome/Dome/Asym/Asym	cDDAA
	5) Asym/Asym/Dome/Asym	cAADA
	6) Dome/Asym/Dome/Asym	cDADA
	7) Asym/Dome/Dome/Asym	cADDA
	8) Dome/Dome/Dome/Asym	cDDDA
	9) Asym/Asym/Asym/Dome	cAAAD
	10) Dome/Asym/Asym/Dome	cDAAD
	11) Asym/Dome/Asym/Dome	cADAD
	12) Dome/Dome/Asym/Dome	cDDAD
	13) Asym/Asym/Dome/Dome	cAADD
	14) Dome/Asym/Dome/Dome	cDADD
	15) Asym/Dome/Dome/Dome	cADDD
	16) Dome/Dome/Dome/Dome	cDDDD

Table 5. Top ranked models for eGB cod with corresponding values for delta AIC, mean recruitment ($\boldsymbol{r}$), mean natural mortality over the last five years ($\overline{M_{1:5,2011+}}, \overline{M_{6+,2011+}}$), relative change in natural mortality for ages 6+ ($\Delta M_{6+} = M_{6+,2015}/M_{6+,1978}$) ($\Delta \boldsymbol{M}_{b_2} = \boldsymbol{M}_{A,T} / \boldsymbol{M}_{A,1}$), and mean fishing mortality before and after 1994 ($\overline{F_{1978:1993}}, \overline{F_{1994+}}$). All models not listed in this table produced biologically implausible results or had delta AIC values greater than 100.

Model	ΔAIC	$\boldsymbol{r}$	$\overline{M_{1:5,2011+}}$	$\overline{M_{6+,2011+}}$	ΔM_{6+}	$\overline{F_{1978:1993}}$	$\overline{F_{1994+}}$
mCon-qCon-sCon-cAAAD	0	11.70	0.37	1.55	6.91	0.40	0.10
mFix-qCon-sCon-cAAAD	11.34	5.78	0.25	1.47	7.80	0.51	0.18
mCon-qCon-sCon-cAAAA	51.33	23.11	0.49	1.54	6.34	0.33	0.07
mCon-qCon-sCon-cAADD	64.34	9.92	0.36	1.45	7.57	0.43	0.13
mFix-qCon-sCon-cAADD	72.56	5.21	0.25	1.37	8.60	0.53	0.21

Table 6. Top ranked models for GB Yellowtail Flounder with corresponding values for delta AIC, mean recruitment (r), mean natural mortality over the last five years ($\overline{M_{1:2,2011+}}, \overline{M_{3+,2011+}}$), relative change in natural mortality for ages 3+ ($\Delta M_{3+} = M_{3+,2015}/M_{3+,1973}$), and mean fishing mortality ($\bar{F}$). All models not listed in this table produced biologically implausible results or had delta AIC values greater than 21.

Model	ΔAIC	r	$\overline{M_{1:2,2011+}}$	$\overline{M_{3+,2011+}}$	ΔM_{3+}	$\overline{F_{1978:1994}}$	$\overline{F_{1995+}}$
mCon-qCon-sCon-cADAD	0	21.96	0.164	1.01	4.13	0.95	0.14
mFix-qCon-sCon-cADAD	1.04	25.69	0.25	1.01	4.01	0.96	0.14
mCon-qCon-sCon-cAAAD	3.74	23.12	0.17	1.06	4.17	0.98	0.14
mFix-qCon-sCon-cAAAD	4.02	26.62	0.25	1.06	4.14	0.99	0.14
mCon-qCon-sCon-cADDD	18.59	20.67	0.15	0.97	4.16	0.92	0.14
mFix-qCon-sCon-cADDD	20.95	24.85	0.25	0.98	4.16	0.93	0.14

Figure 1. Age-composition data for eGB cod. Every 5th age class is displayed as a red circle.

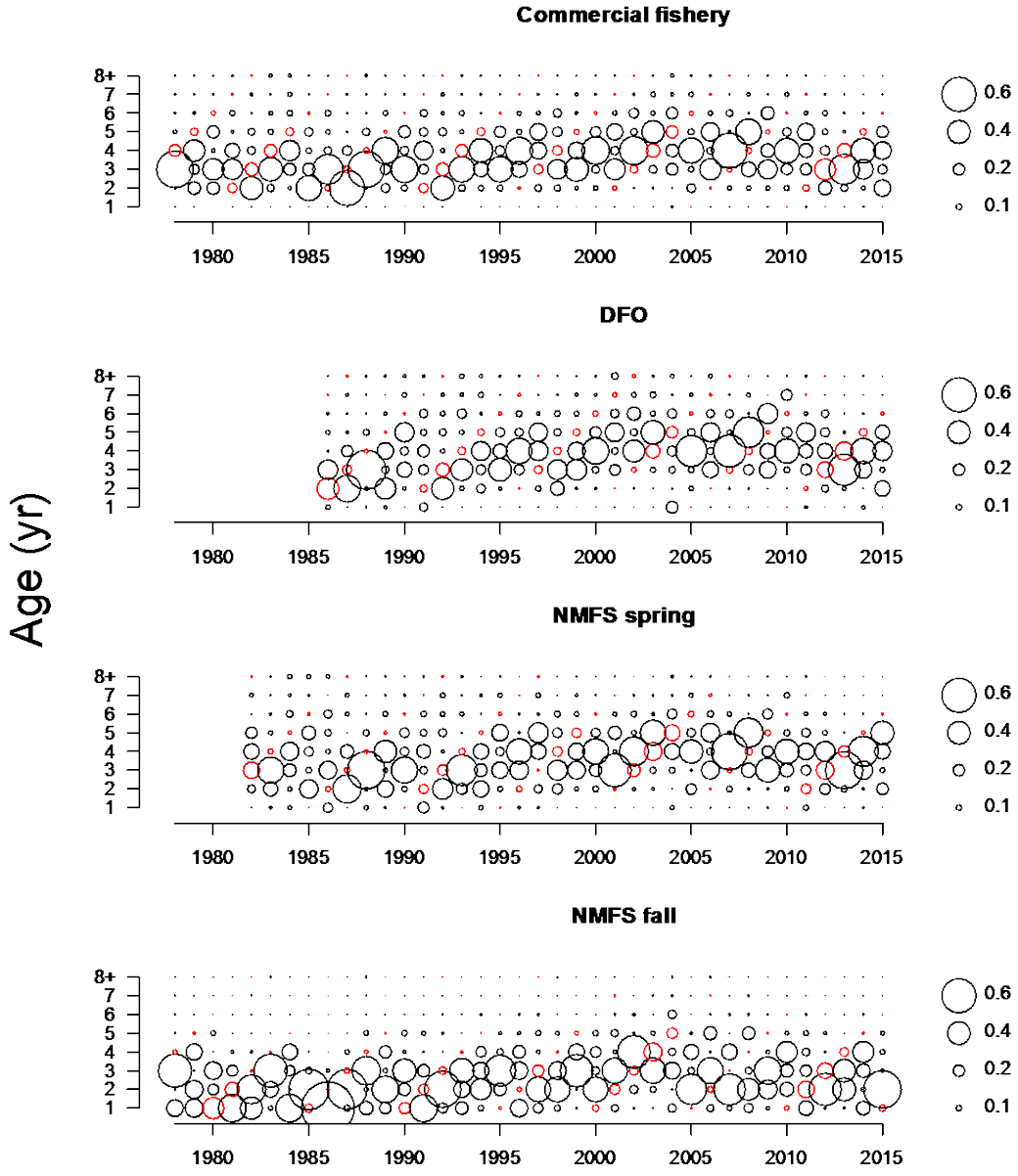

Figure 2. Age-composition data for GB Yellowtail Flounder. Every 5th age class is displayed as a red circle

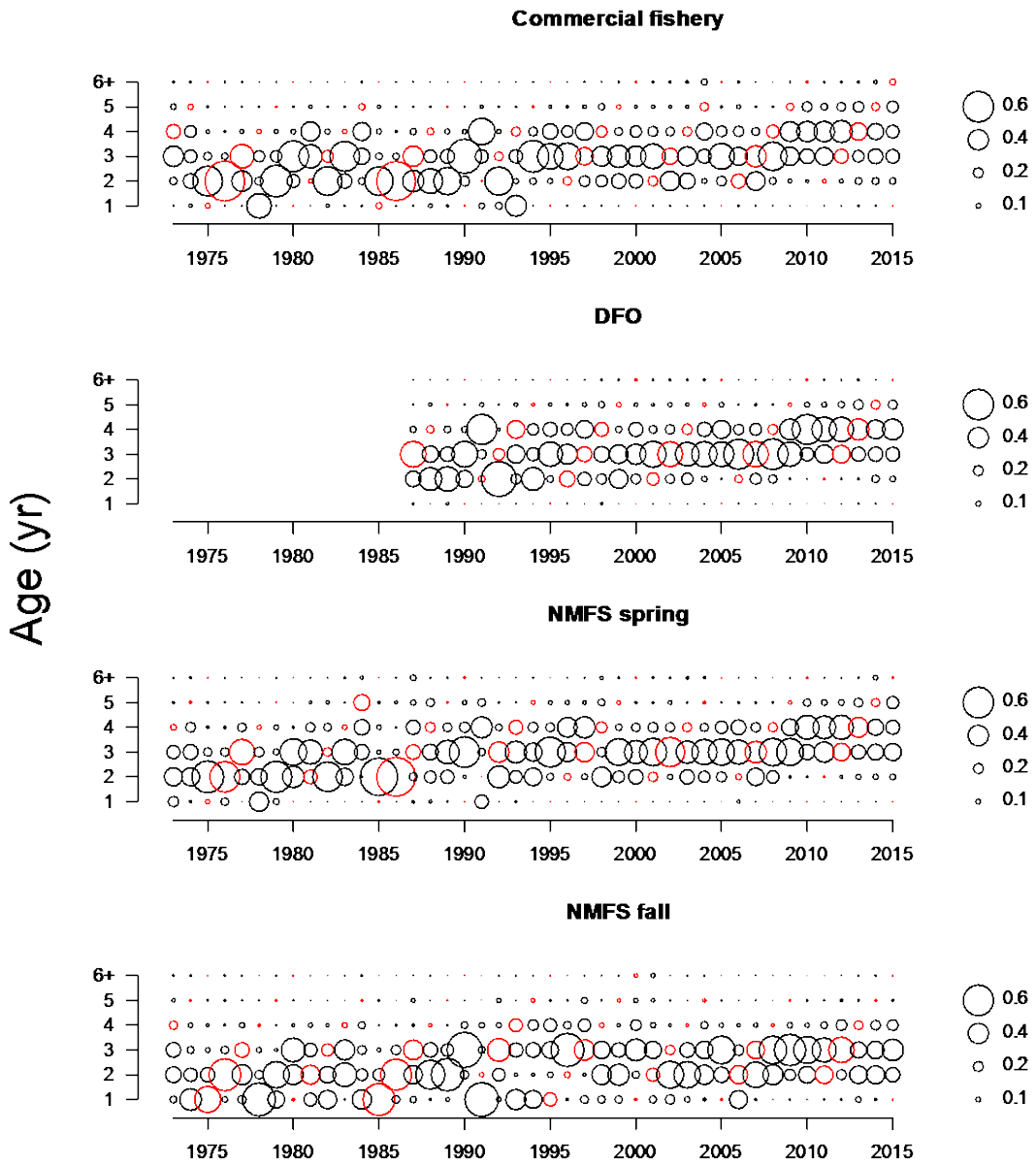

Figure 3. Diagnostics for eGB cod model mCon-qCon-sCon-cAAAD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

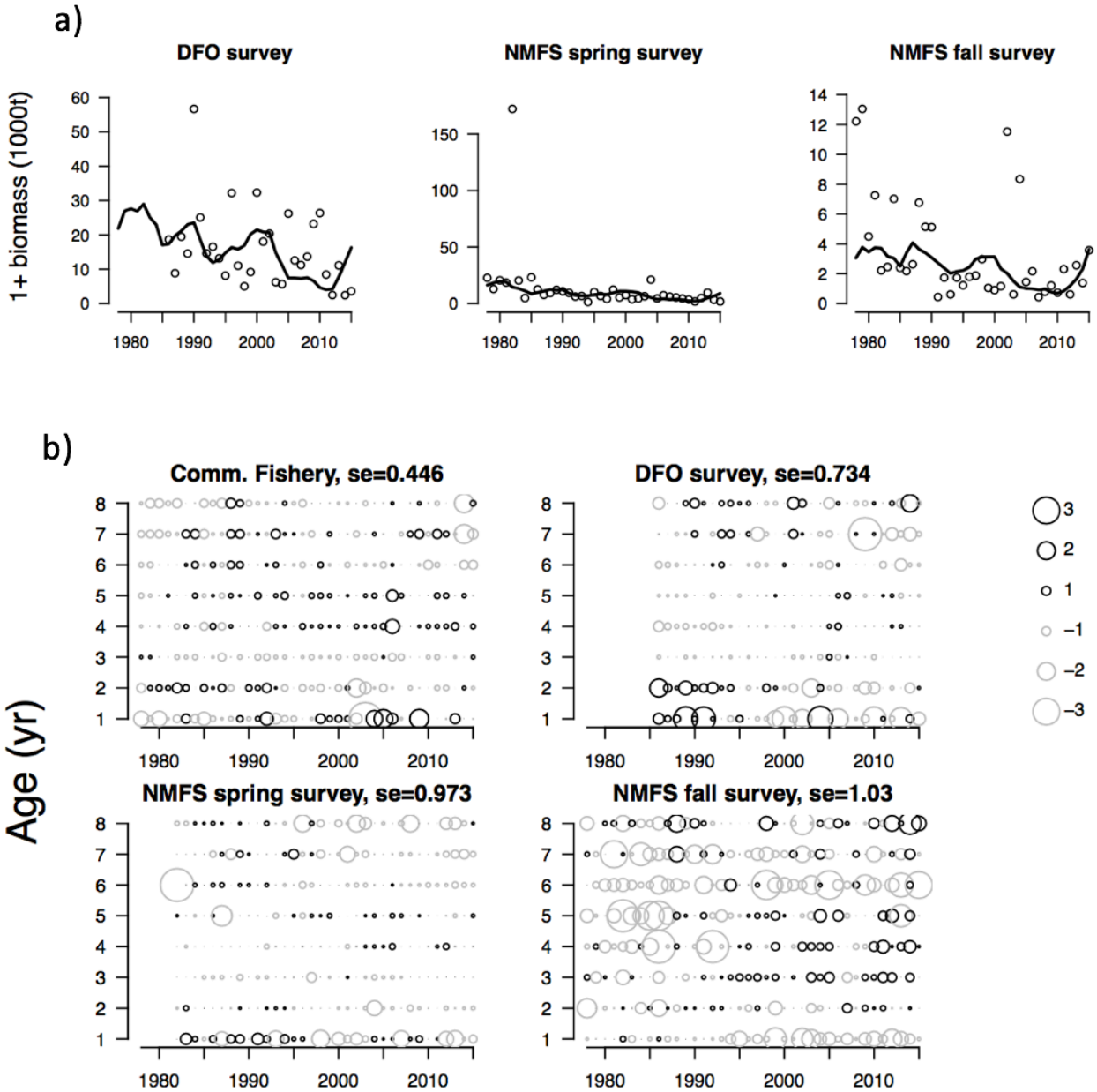

Figure 4. Output from eGB cod model mCon-qCon-sCon-cAAAD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

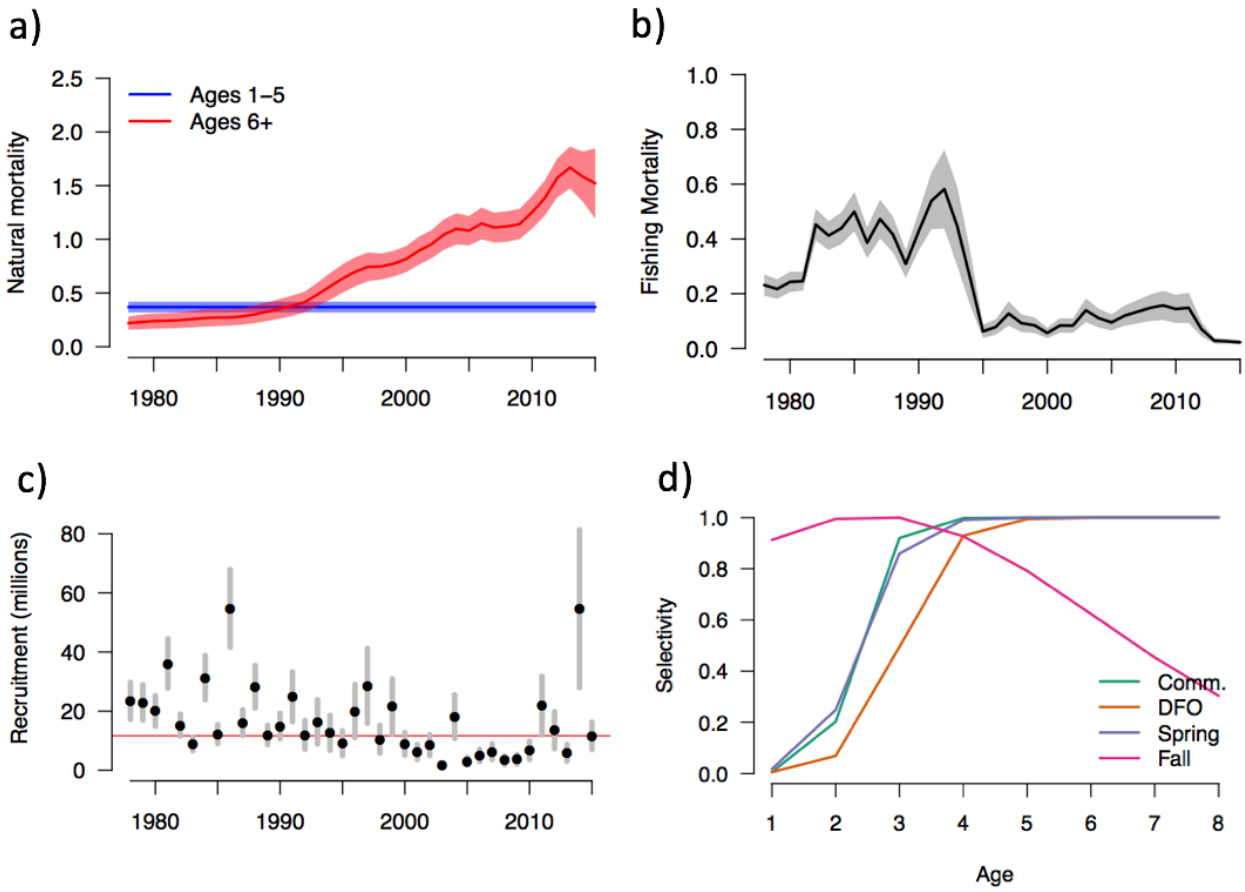

Figure 5. Retrospective analysis for eGB cod model mCon-qCon-sCon-cAAAD.

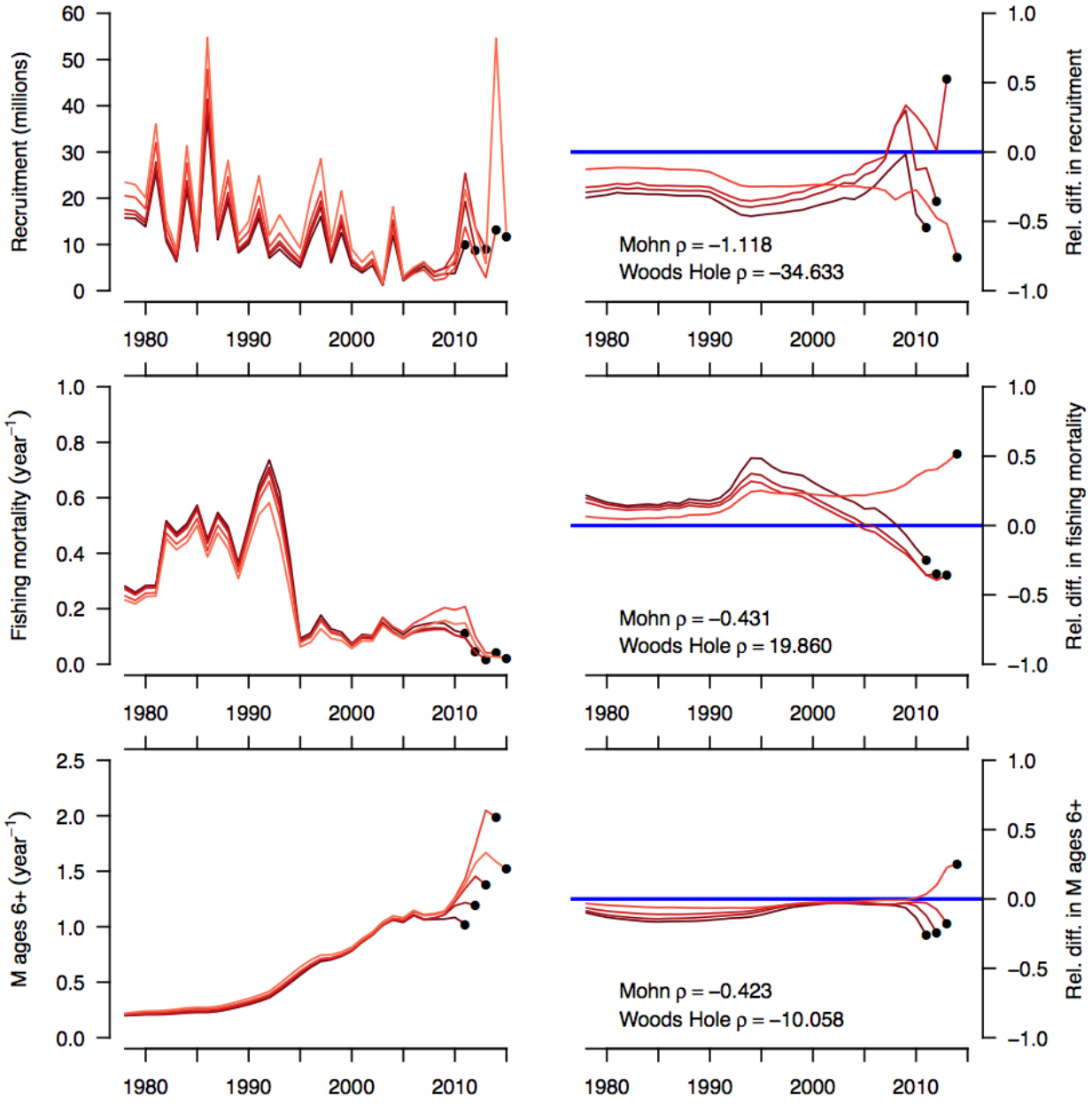

Figure 6. Diagnostics for eGB cod model mFix-qCon-sCon-cAAAD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

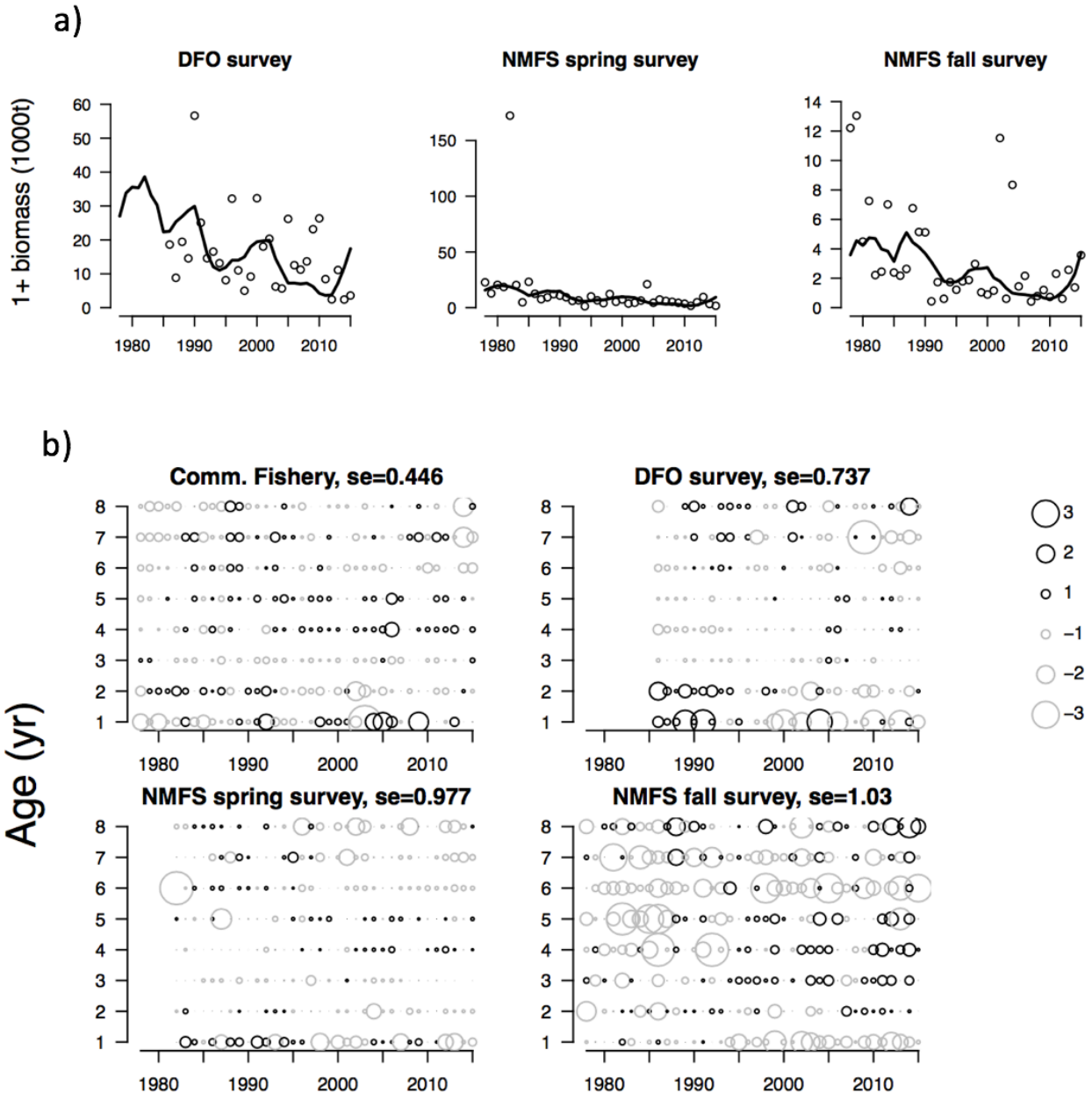

Figure 7. Output from eGB cod model mFix-qCon-sCon-cAAAD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

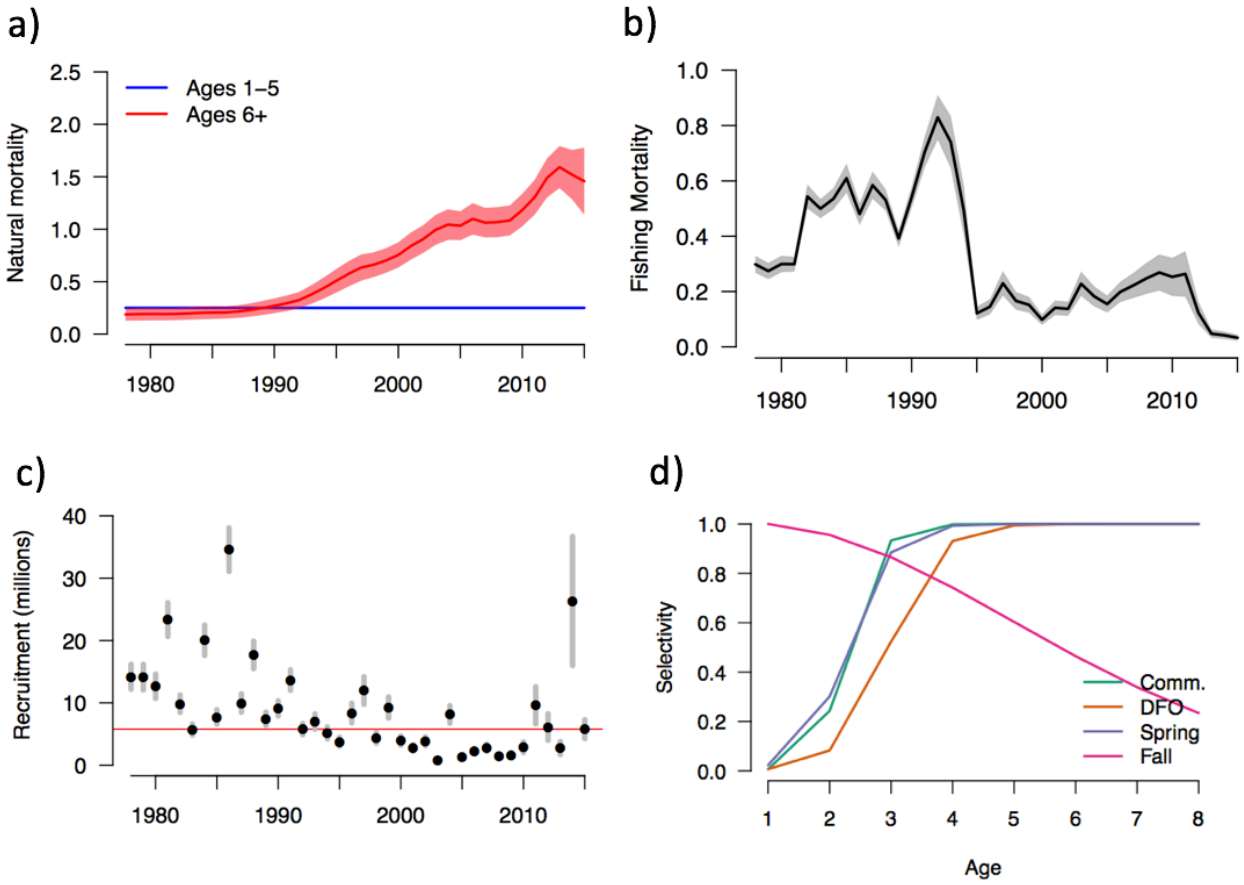

Figure 8. Retrospective analysis for eGB cod model mFix-qCon-sCon-cAAAD.

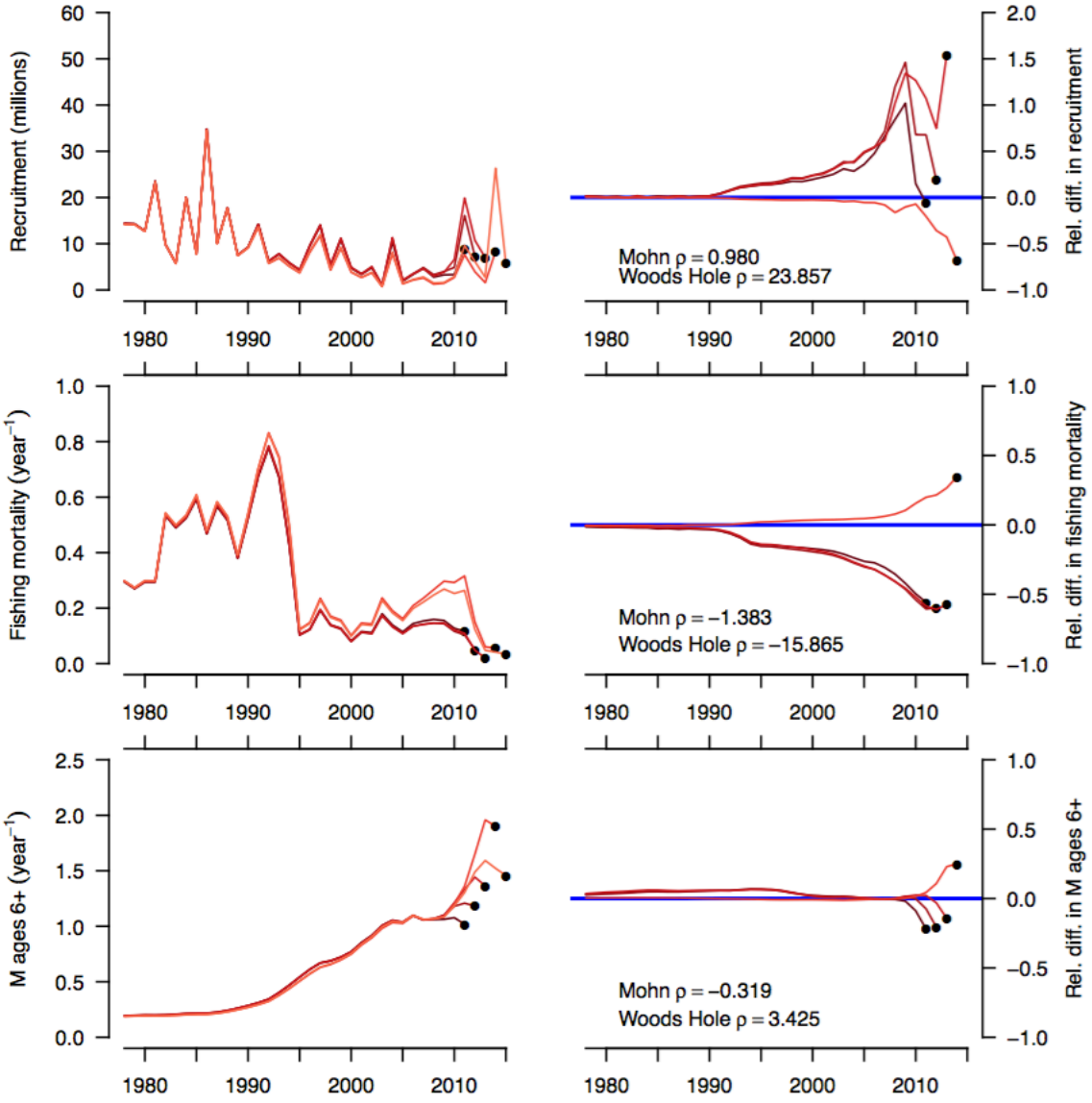

Figure 9. Diagnostics for eGB cod model mCon-qCon-sCon-cAAAA including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

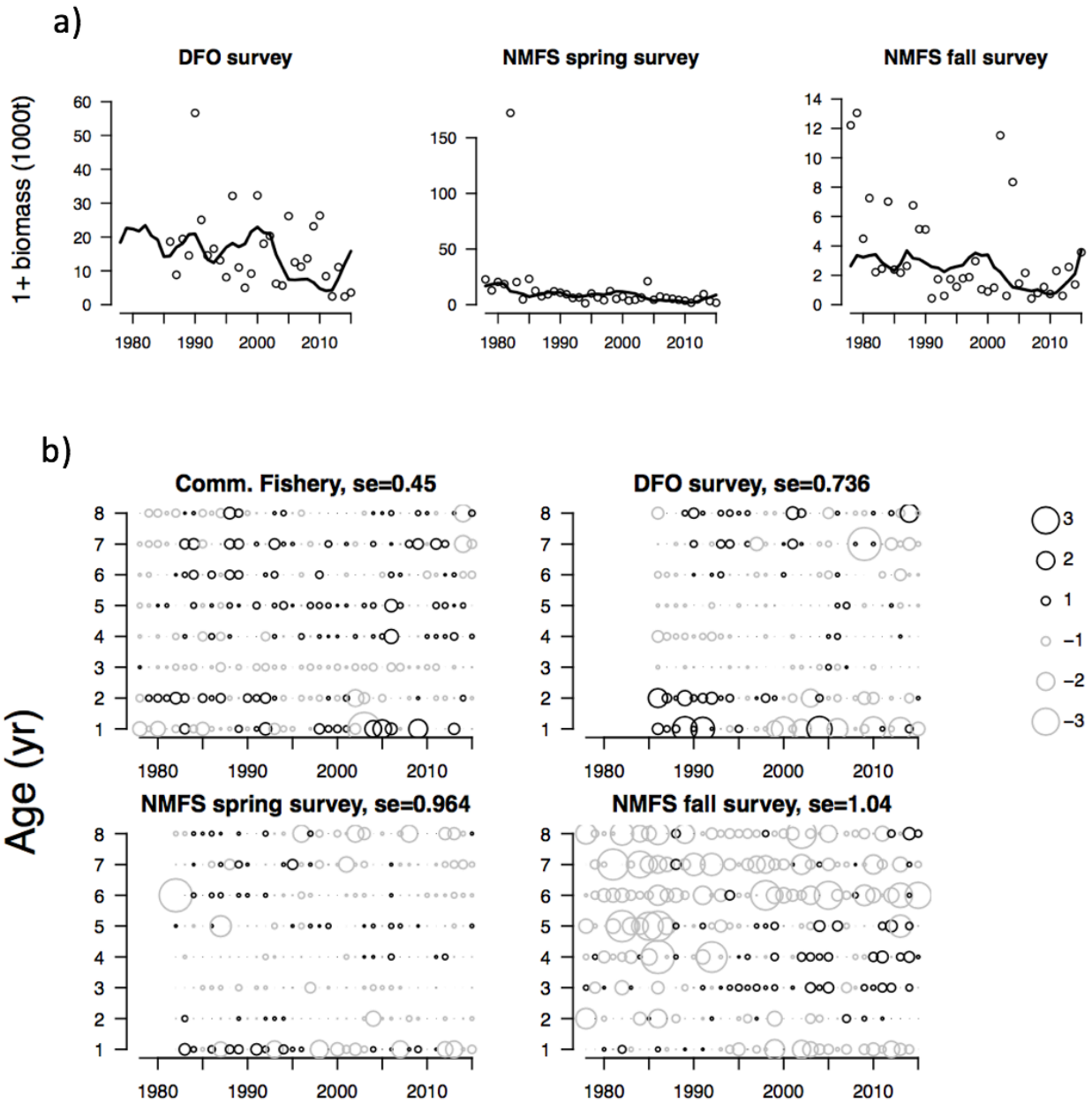

Figure 10. Output from eGB cod model mCon-qCon-sCon-cAAAA including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

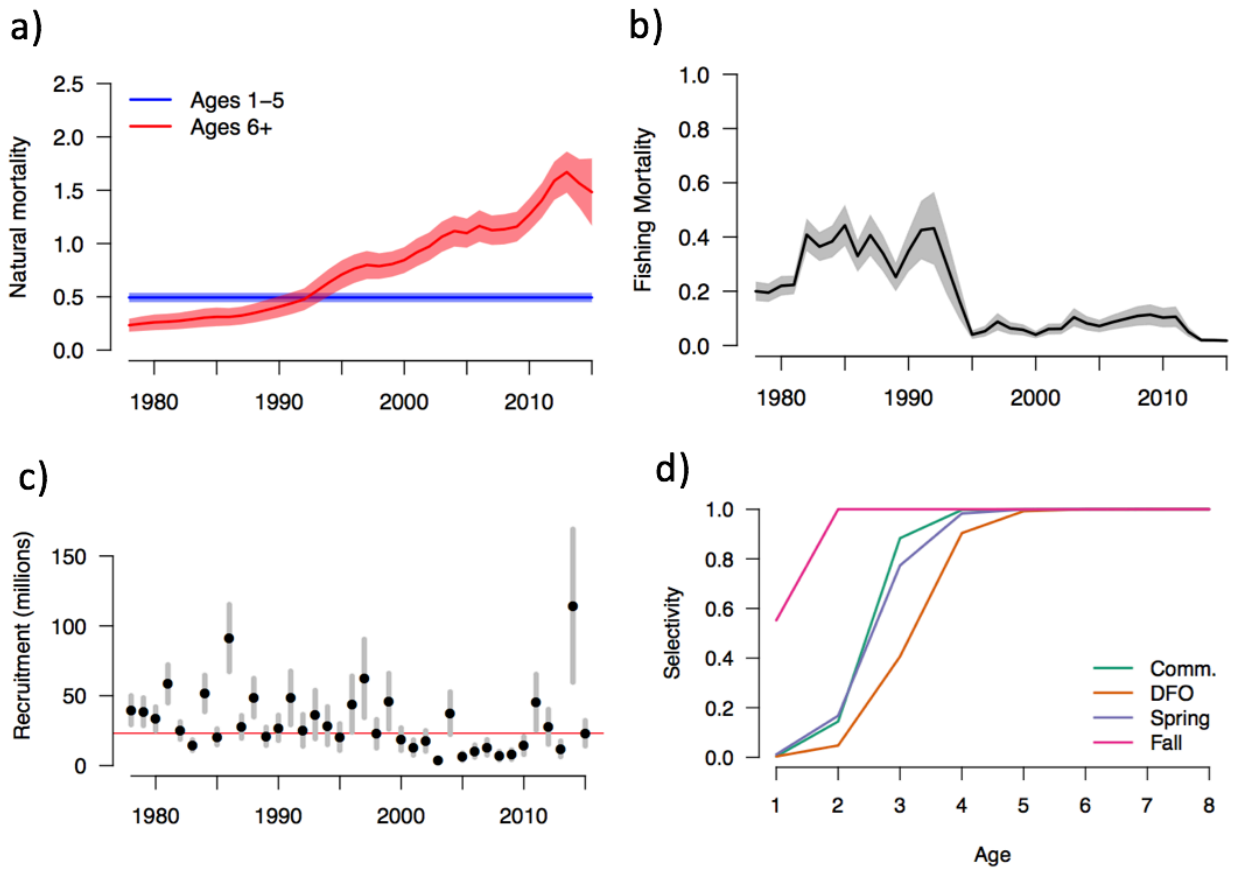

Figure 11. Retrospective analysis for eGB cod model mCon-qCon-sCon-cAAAA.

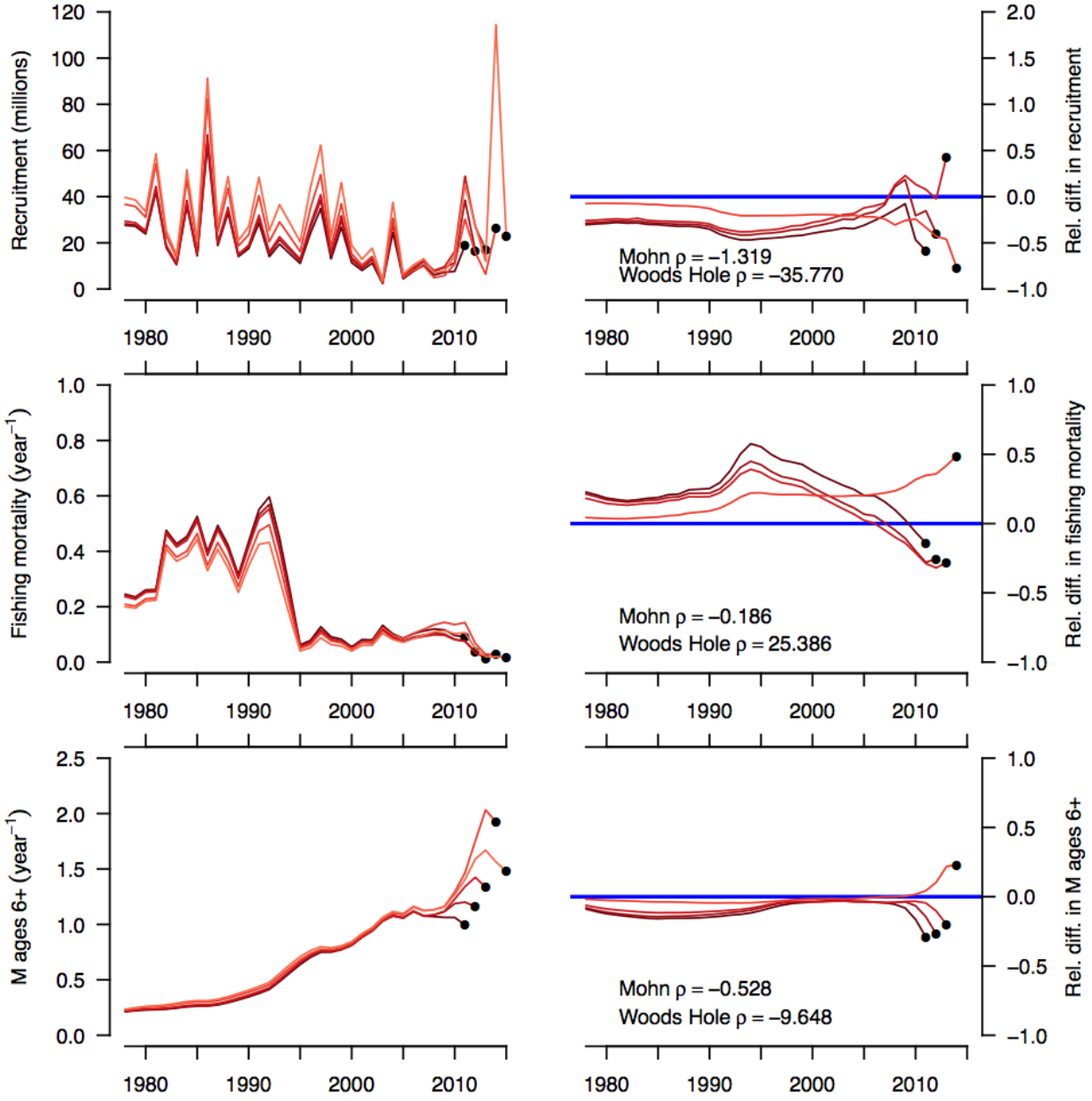

Figure 12. Diagnostics for eGB cod model mCon-qCon-sCon-cAADD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

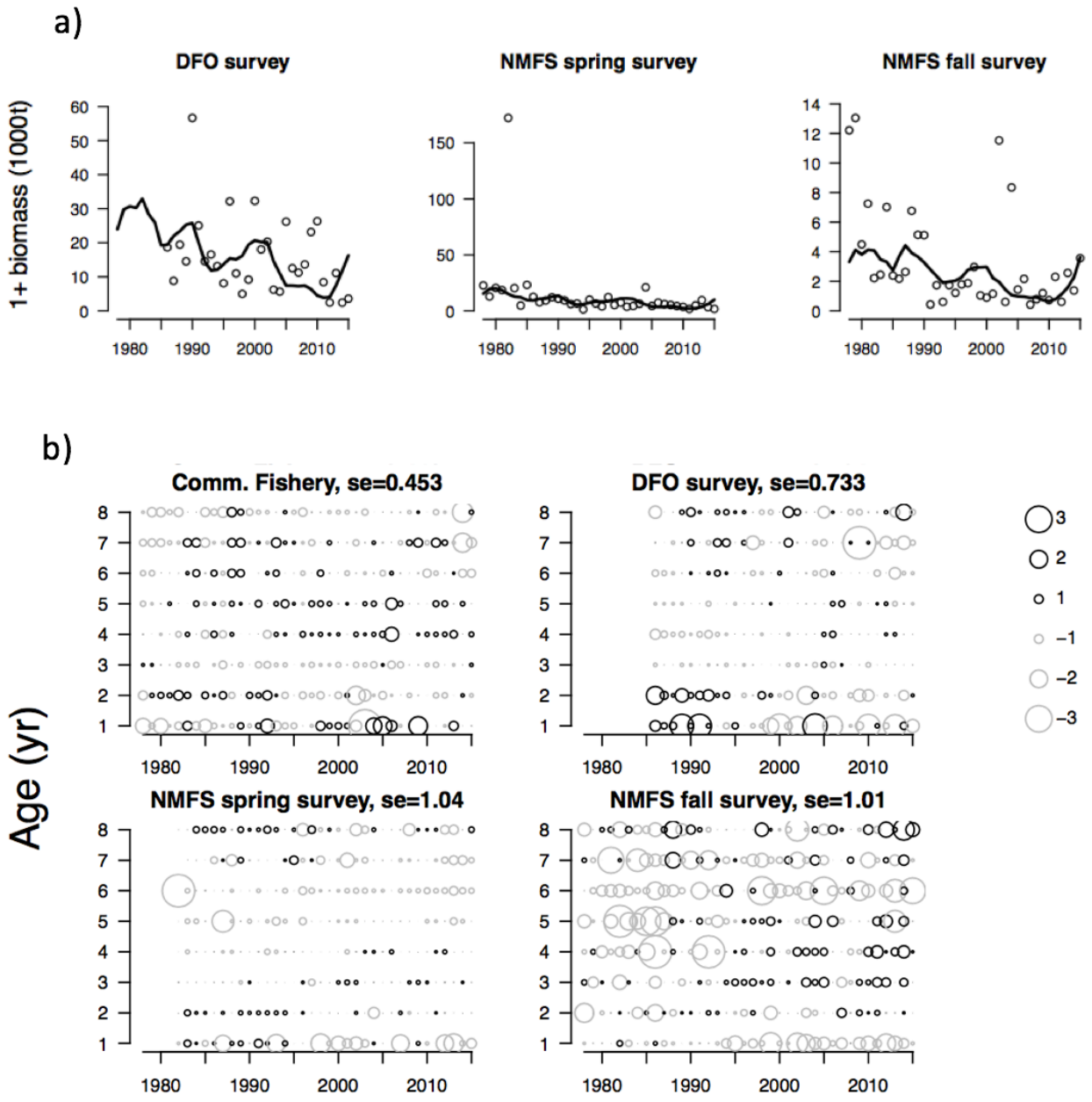

Figure 13. Output from eGB cod model mCon-qCon-sCon-cAADD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

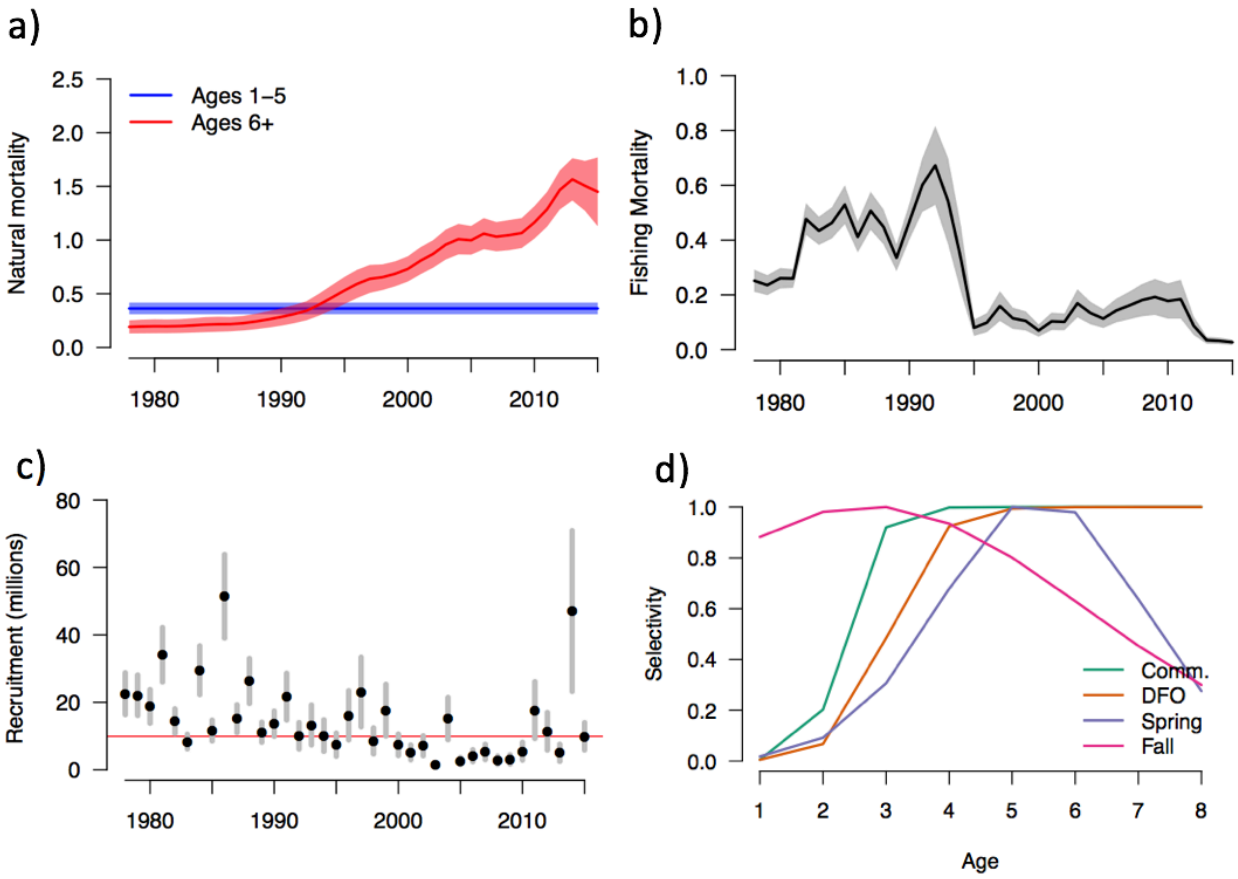

Figure 14. Retrospective analysis for eGB cod model mCon-qCon-sCon-cAADD.

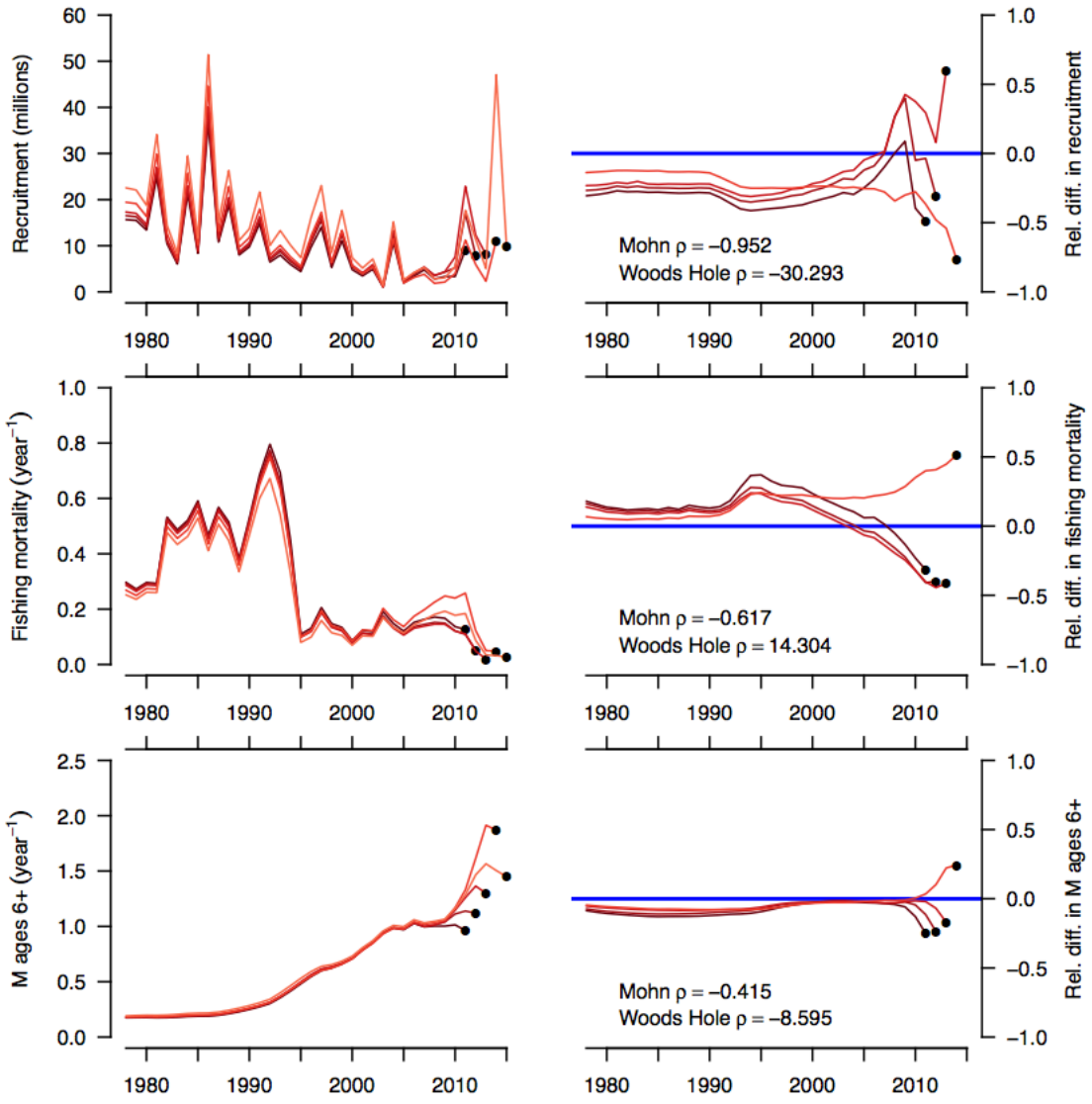

Figure 15. Diagnostics for eGB cod model mCon-qCon-sCon-cAADD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

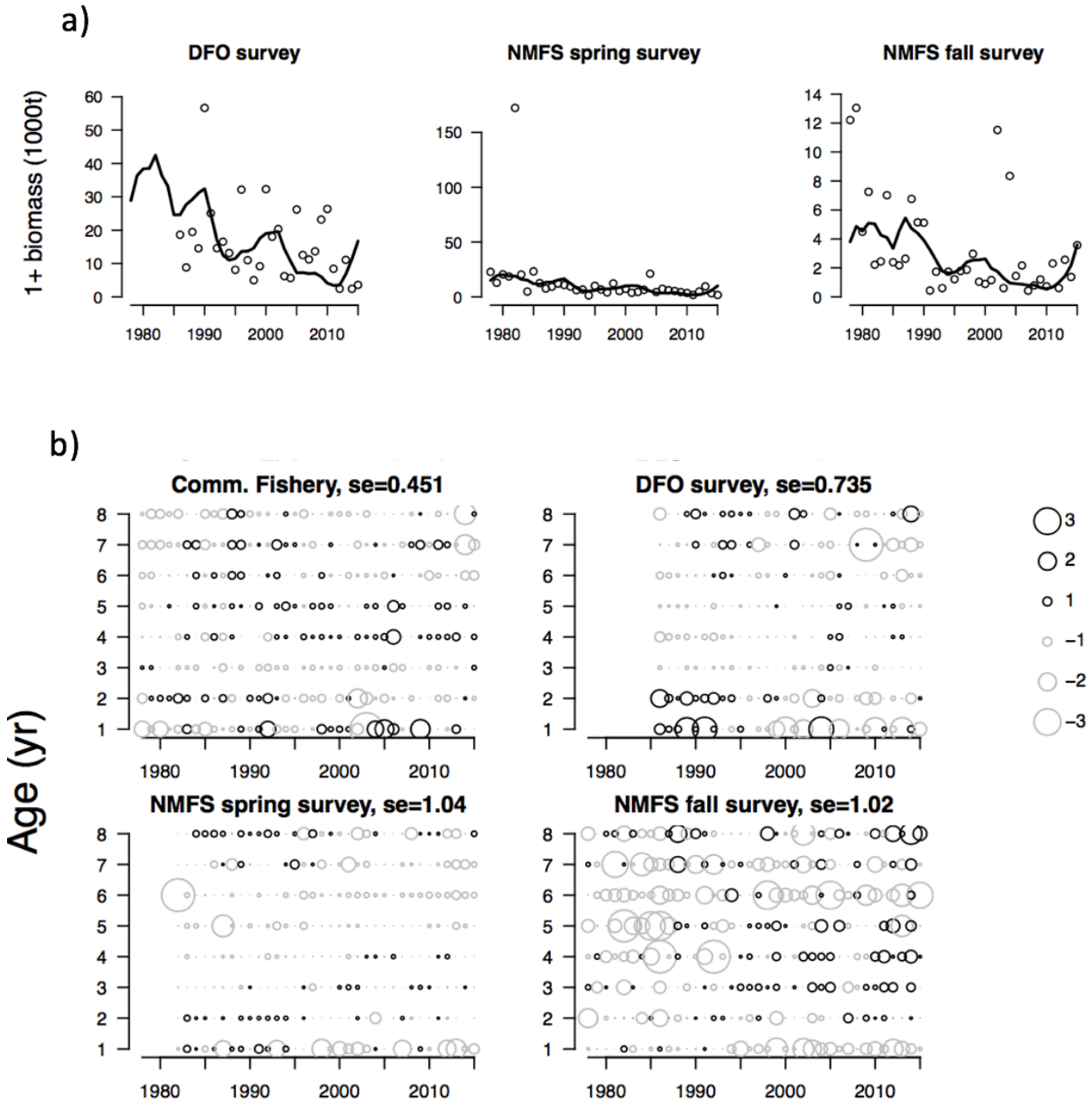

Figure 16. Output from eGB cod model mFix-qCon-sCon-cAADD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

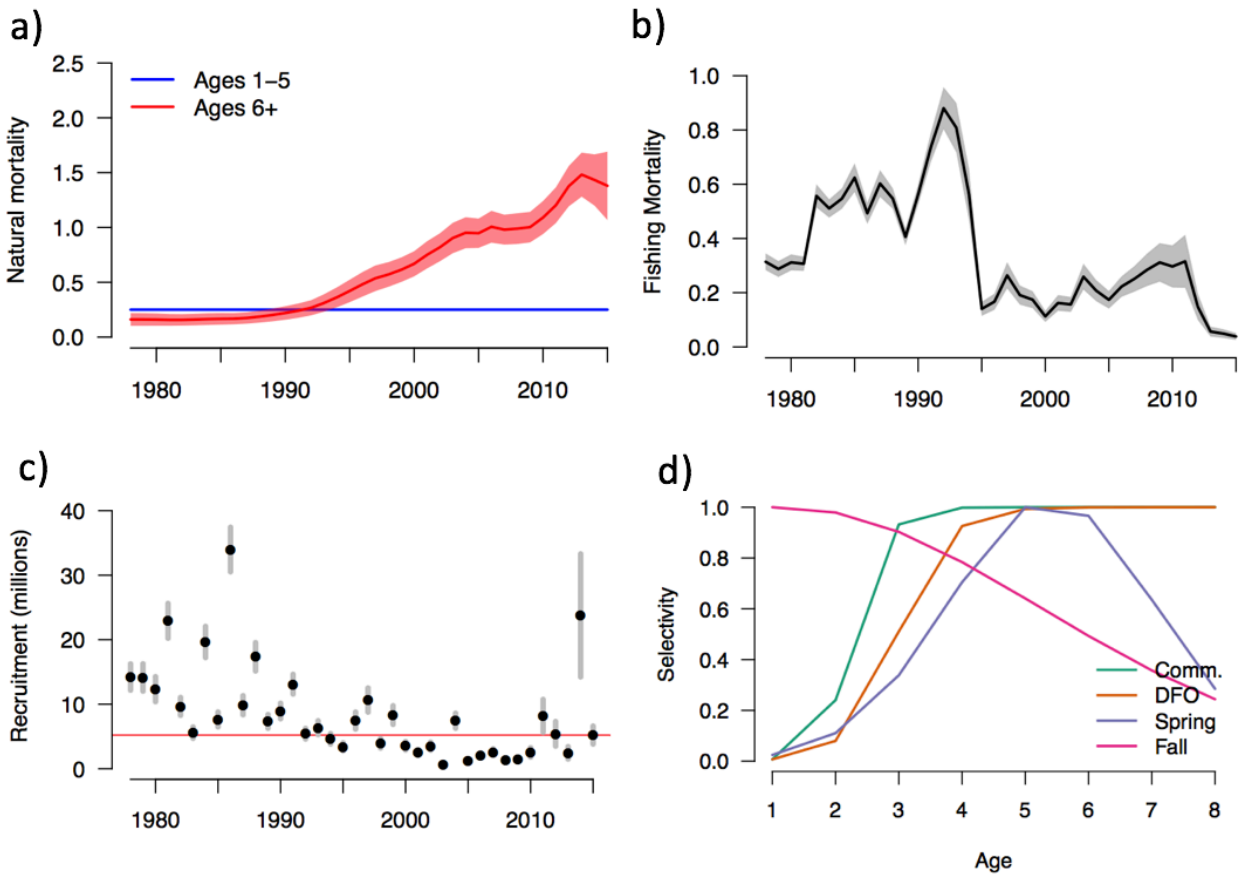

Figure 17. Retrospective analysis for eGB cod model mFix-qCon-sCon-cAADD.

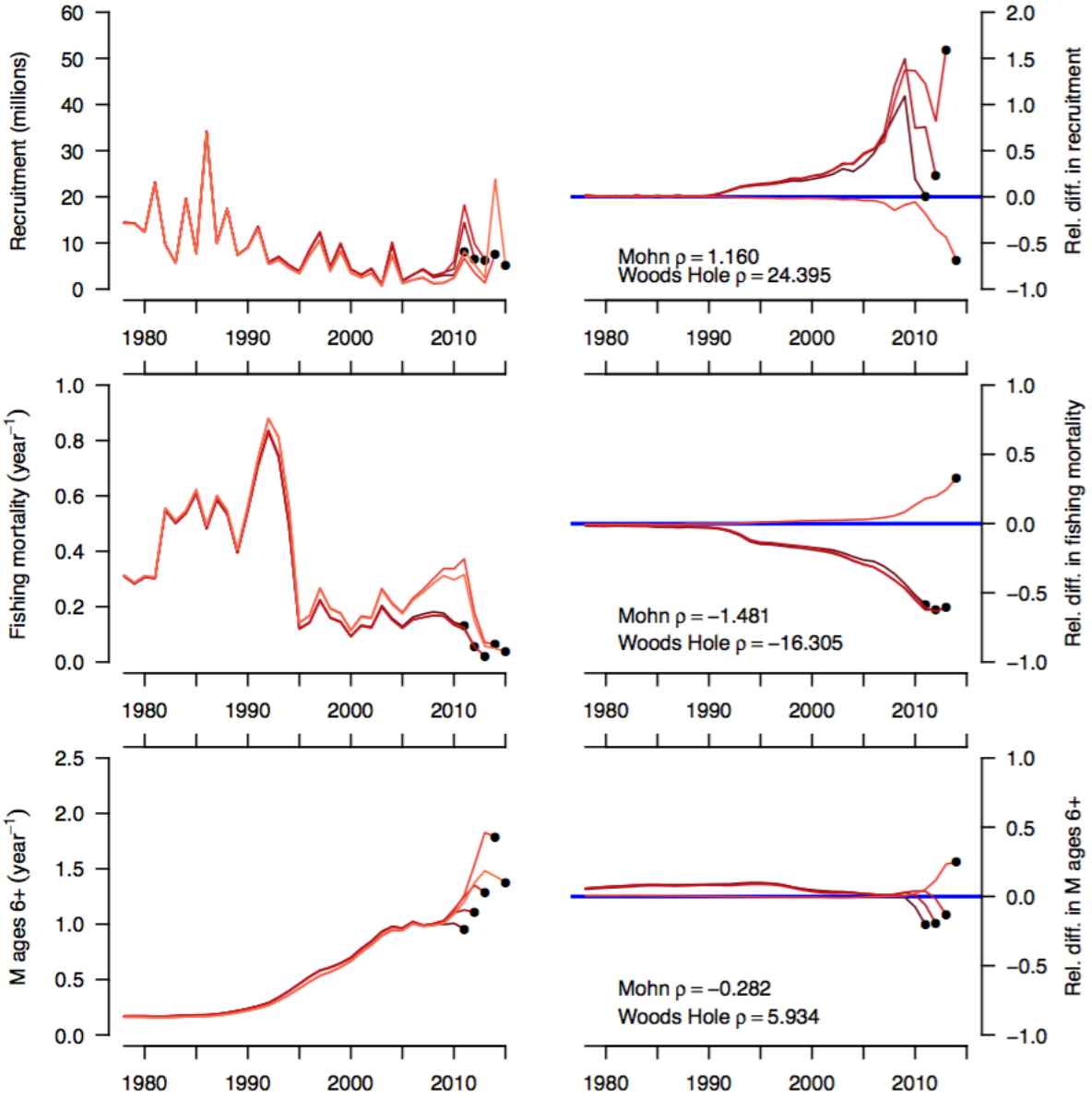

Figure 18. Diagnostics for GB Yellowtail Flounder model mCon-qCon-sCon-cADAD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

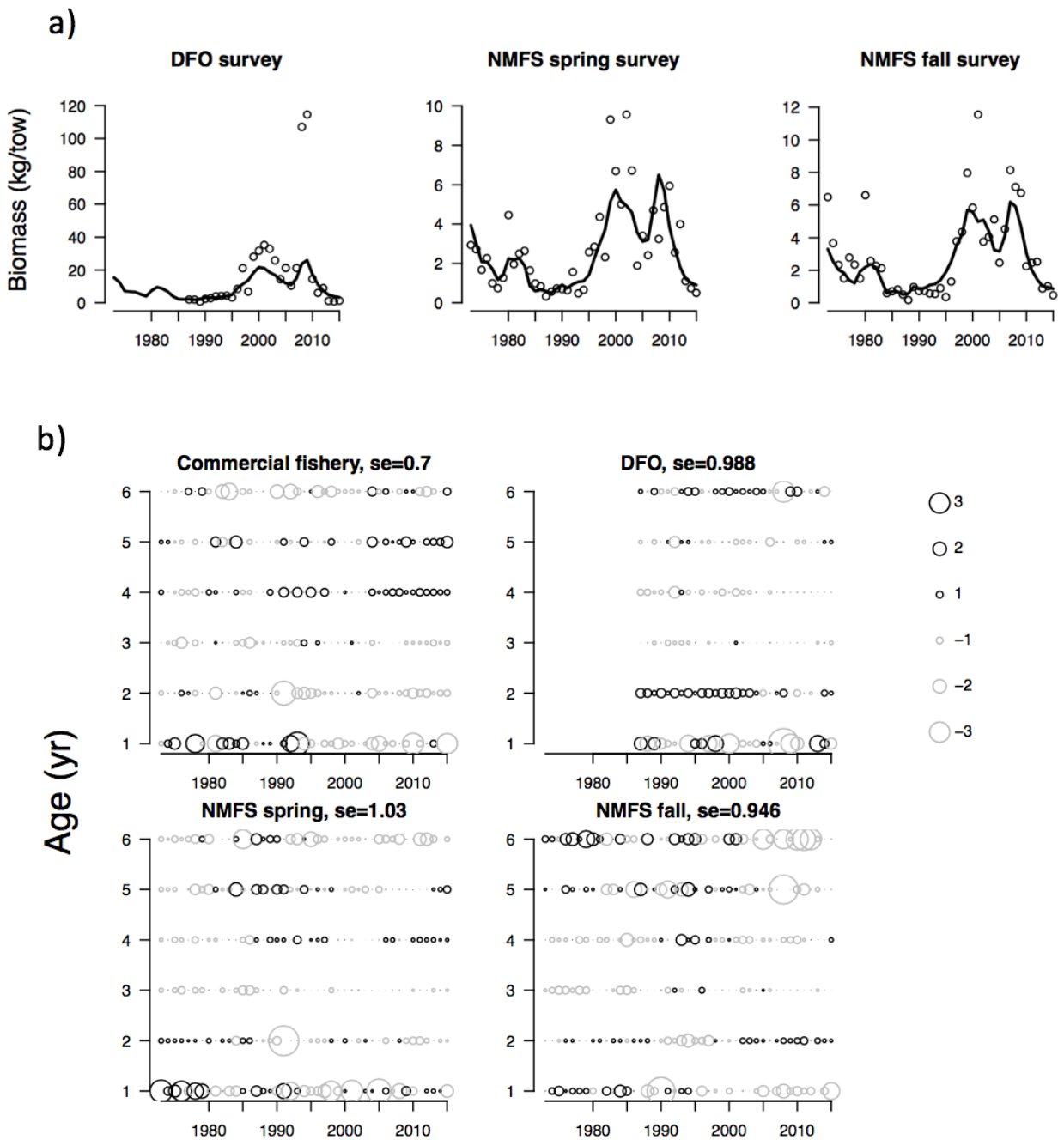

Figure 19. Output from GB Yellowtail Flounder model mCon-qCon-sCon-cADAD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

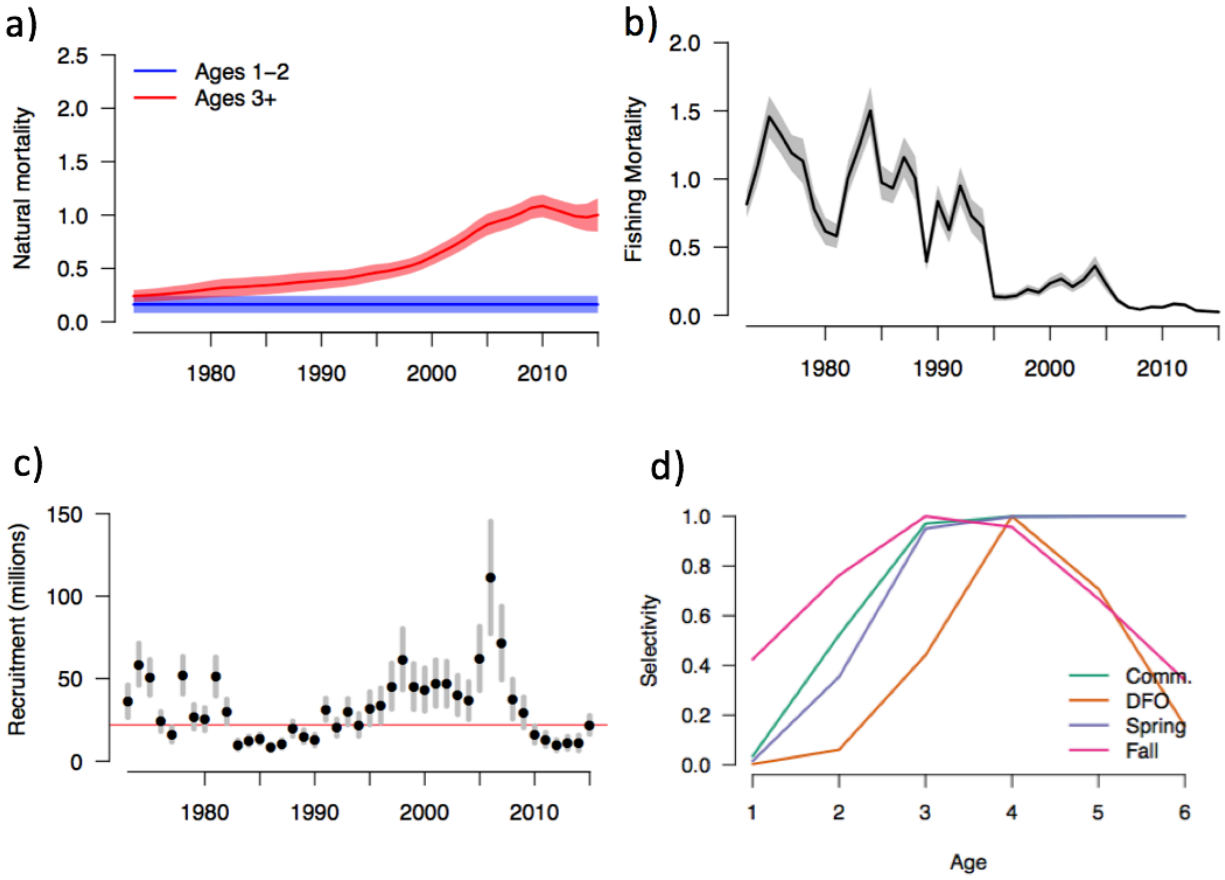

Figure 20. Retrospective analysis for GB Yellowtail Flounder model mCon-qCon-sCon-cADAD.

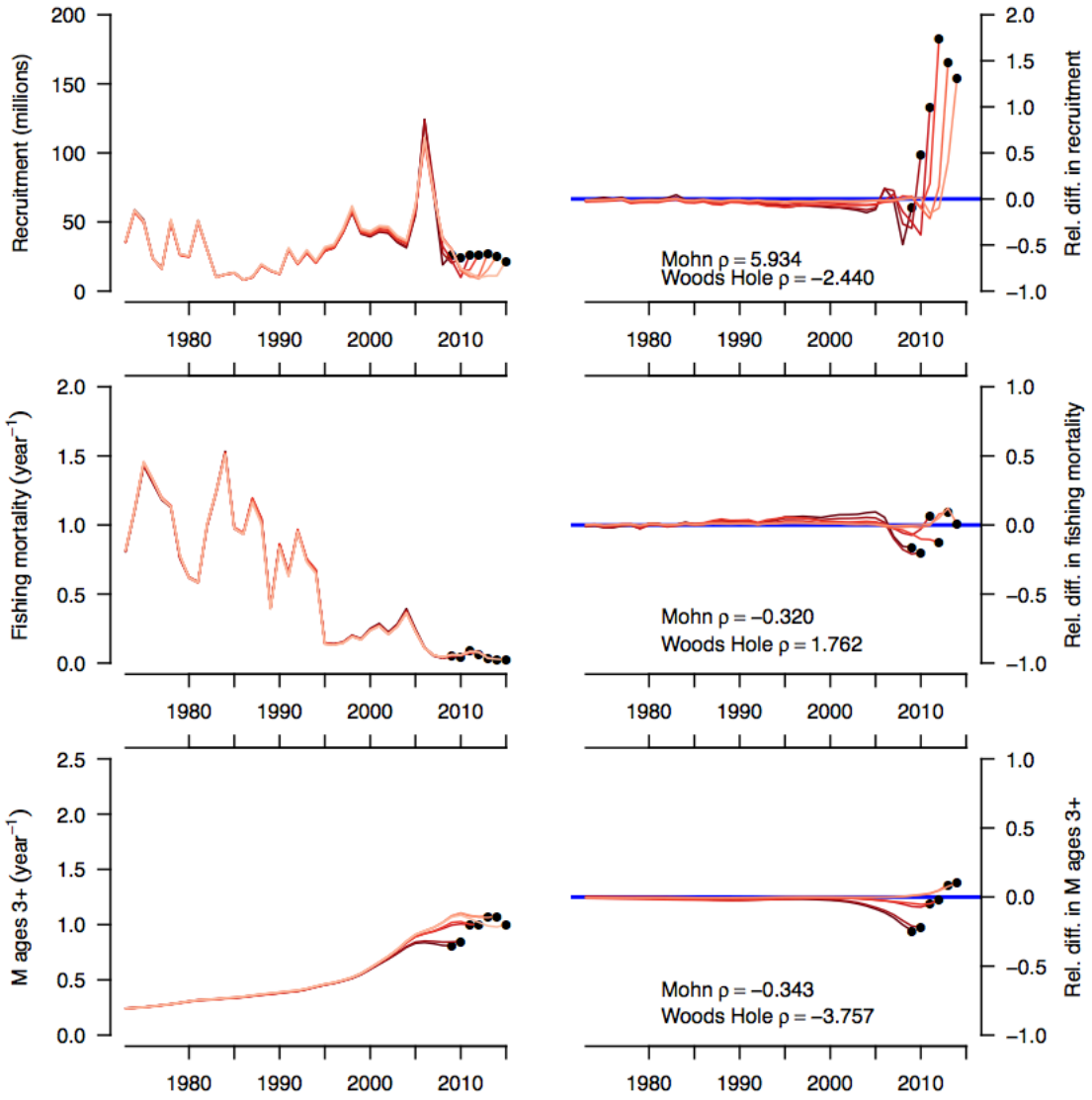

Figure 21. Diagnostics for GB Yellowtail Flounder model mFix-qCon-sCon-cADAD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

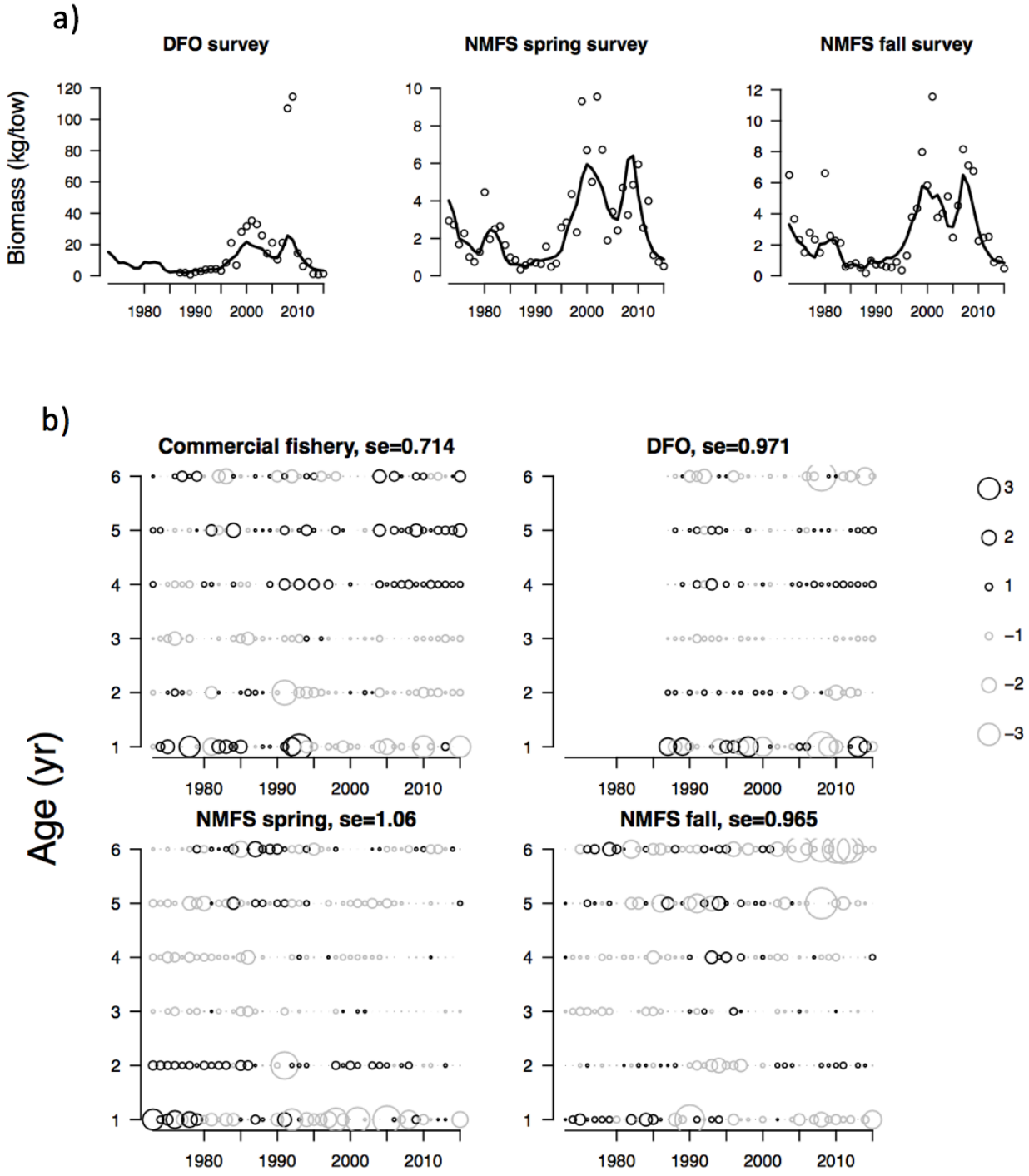

Figure 22. Output from GB Yellowtail Flounder model mFix-qCon-sCon-cADAD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

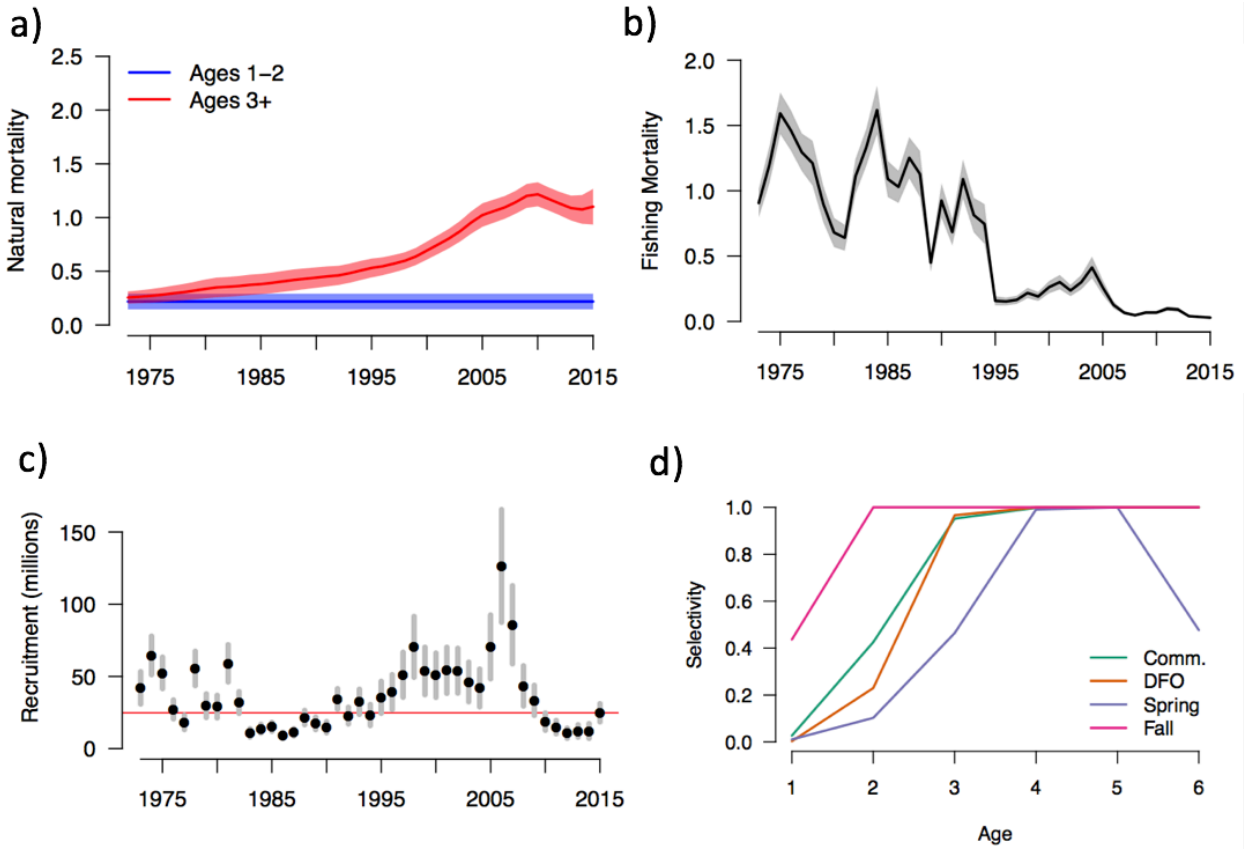

Figure 23. Retrospective analysis for GB Yellowtail Flounder model mFix-qCon-sCon-cADAD.

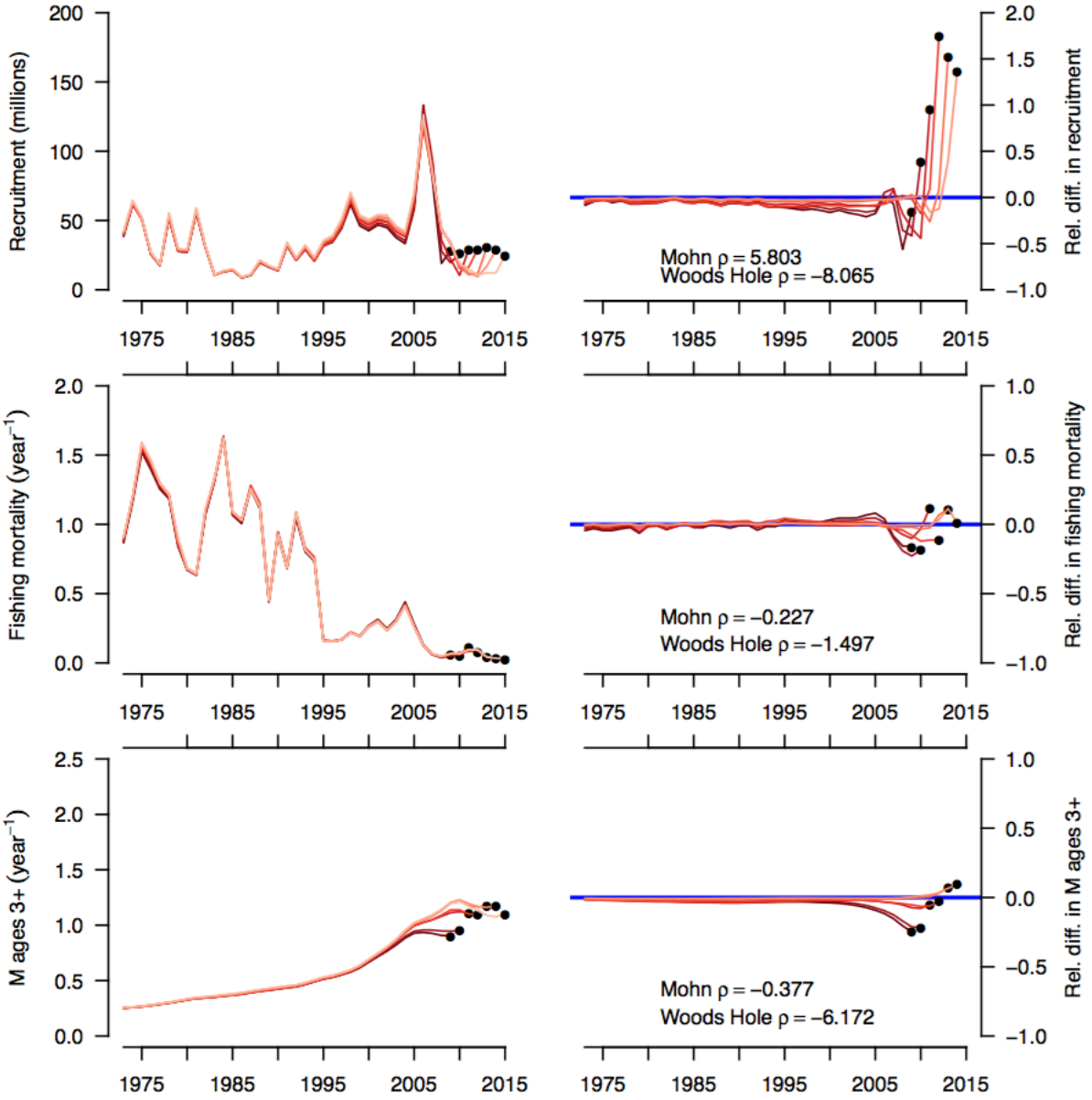

Figure 24. Diagnostics for GB Yellowtail Flounder model mCon-qCon-sCon-cAAAD including (a) model fits (lines) to observed abundance indices (circles) and (b) age-composition residuals (observed-estimated).

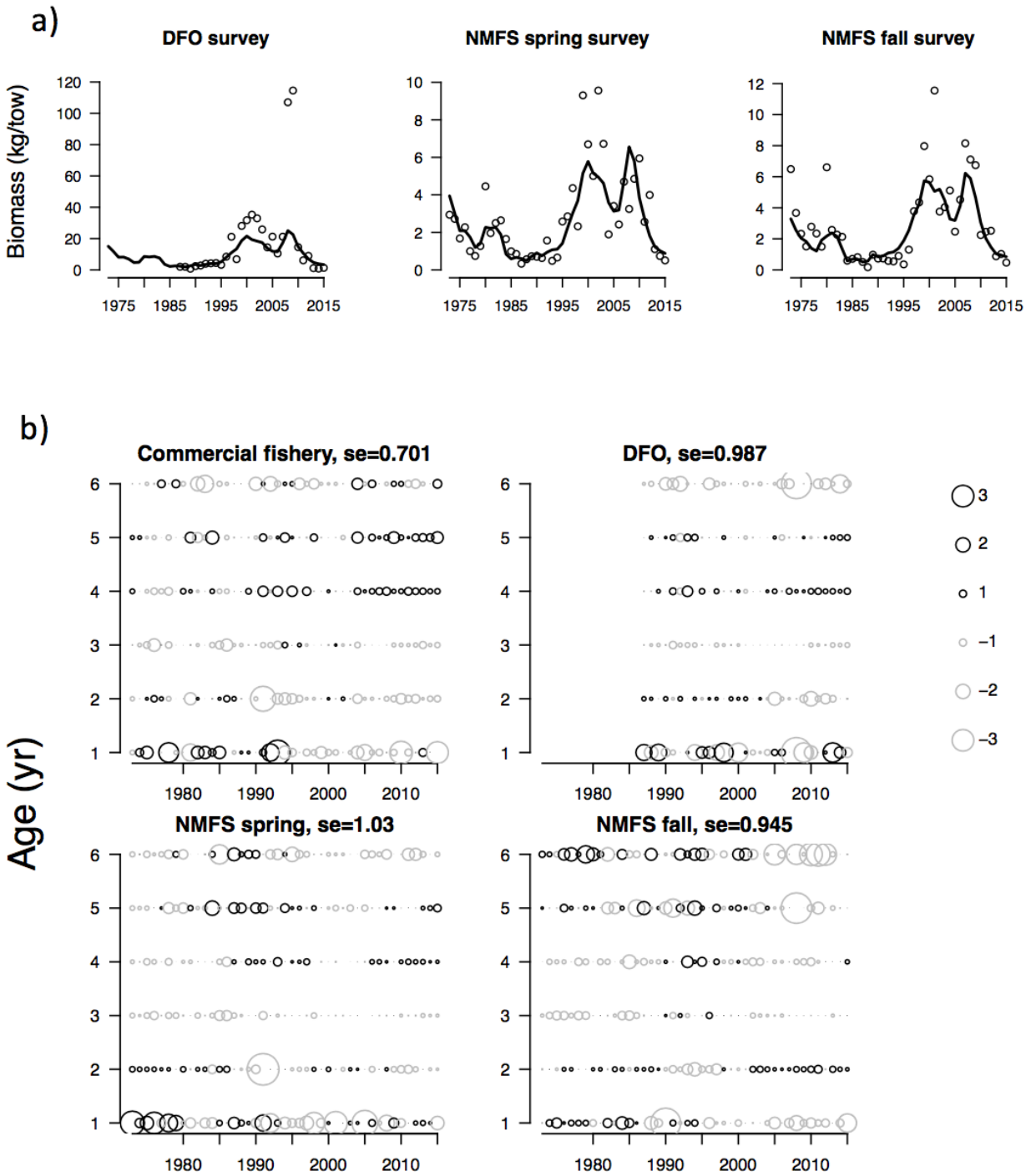

Figure 25. Output from GB Yellowtail Flounder model mCon-qCon-sCon-cAAAD including a) natural mortality, b) fishing mortality, c) recruitment, and d) selectivity. Shaded regions in a and b indicate 90% confidence intervals. The red line in c indicates mean recruitment while the grey bars indicate 90% confidence intervals.

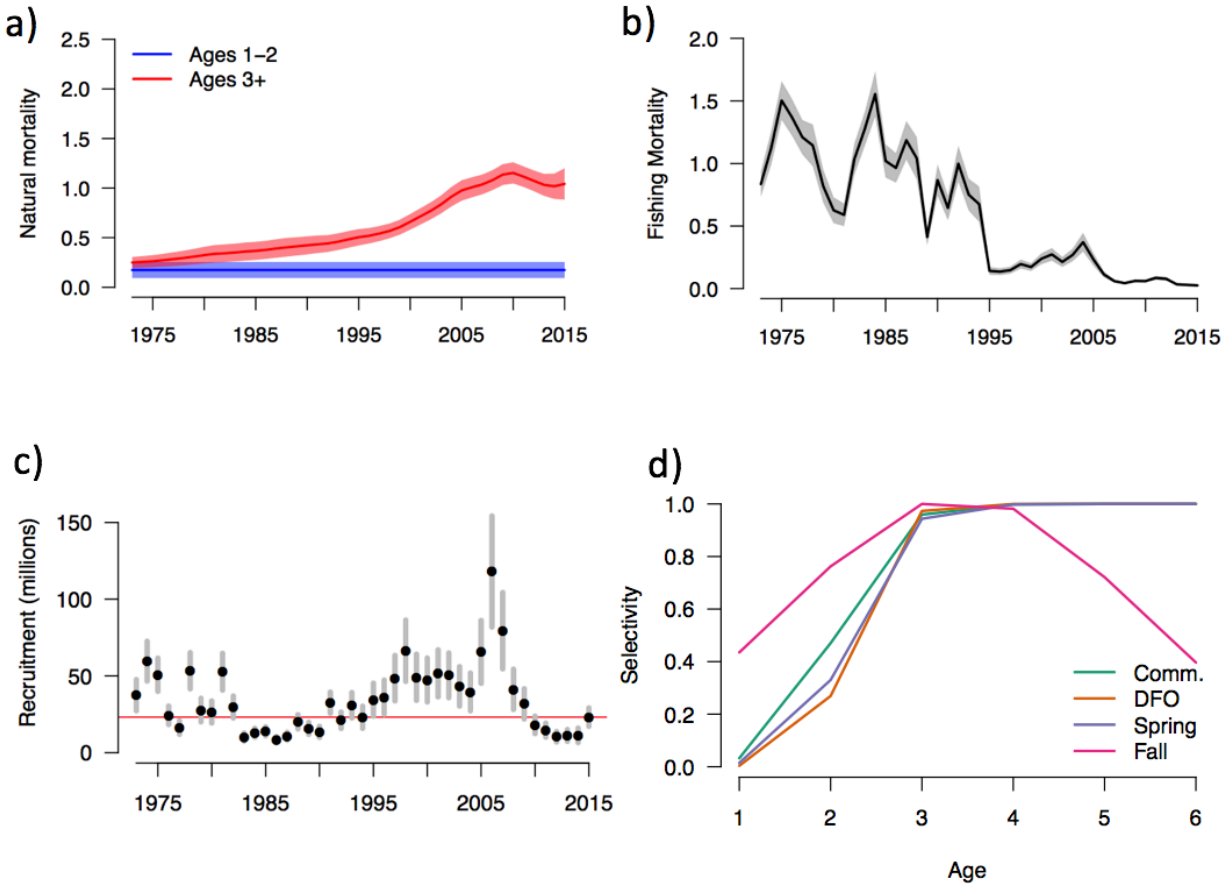
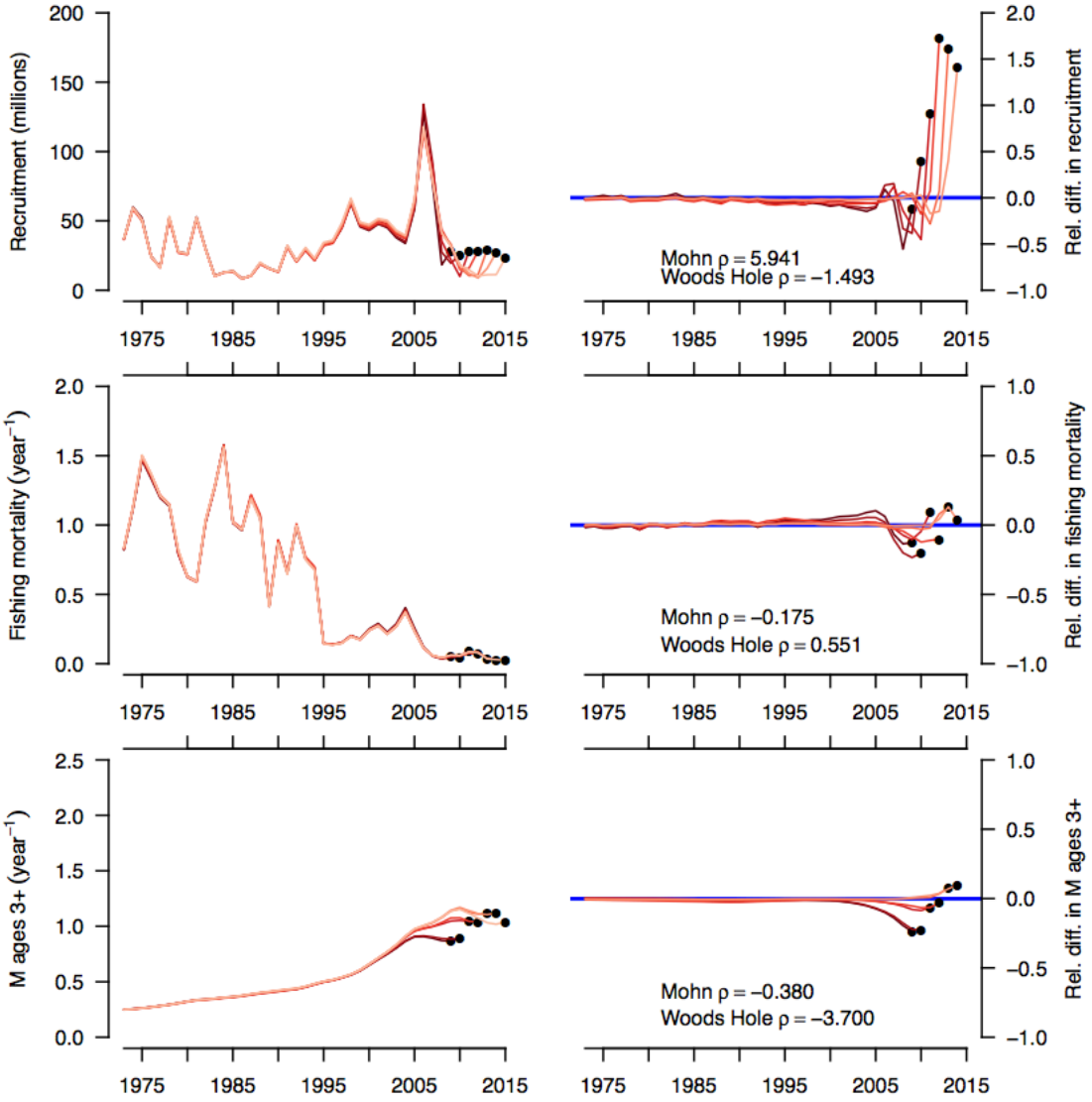
Figure 26. Retrospective analysis for GB Yellowtail Flounder model mCon-qCon-sCon-cAAAD.