

A linked separable–ADAPT VPA assessment model for western horse mackerel (*Trachurus trachurus*), accounting for realized fecundity as a function of fish weight

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The western horse mackerel stock covers a large area of the Northeast Atlantic and is characterized by the sporadic occurrence of strong year classes. The only fishery-independent data available for its assessments are the estimates of total annual egg production from triennial egg surveys. Horse mackerel are indeterminate spawners, so a direct conversion of total annual egg production to spawning-stock biomass using prespawning-season estimates of fecundity is not viable. There is also evidence that potential fecundity per kg spawning female increases with fish weight. A linked separable–ADAPT VPA (SAD) model was developed that combines data on total catch, catch-at-age, and total annual egg production with data on potential and realized fecundity to provide population estimates for western horse mackerel. The model accounts for potential fecundity as a function of fish weight and for the development of a targeted fishery on the strong 1982 year class. Simulations confirm that the SAD model is able to reproduce population estimates without bias under a range of scenarios, except where there is a trend in realized fecundity. This underscores the need for improved information on realized fecundity, or alternatively the need to develop management plans that are robust to this source of uncertainty.

Keywords: potential fecundity, realized fecundity, separable–ADAPT VPA, simulation, stock assessment, western horse mackerel.

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Introduction

Atlantic horse mackerel (*Trachurus trachurus*) are widely distributed throughout the Northeast Atlantic from Norway to the Cape Verde Islands and extending into the Mediterranean Sea (Abaunza *et al.*, 2008). The International Council for the Exploration of the Sea (ICES) recognizes three stocks in the Northeast Atlantic based on egg distributions, temporal and spatial distributions of the fishery, and the results from the EU-funded project HOMSIR (QLK5-CT1999-01438), which integrated a variety of approaches to investigate stock identification (Abaunza *et al.*, 2008; ICES, 2008a). The southern stock is found in the Atlantic waters of the Iberian Peninsula, the North Sea stock in the eastern English Channel and North Sea, and the western stock on the northeast continental shelf of Europe, stretching from northern Spain to Norway (Figure 1). Over the period 2000–2007, catches fluctuated between 190 000 and 280 000 t (ICES, 2008a). Catches from the western stock averaged some 176 000 t over the period 2000–2007, accounting for the bulk of catches (average 74%) from these three stocks (ICES, 2008a). We focus on the western stock.

Western horse mackerel have a long spawning season with a peak in late spring/early summer (Abaunza *et al.*, 2003). They spawn in the Bay of Biscay and southwest of the British Isles (“juvenile area” in Figure 1). Age and length distributions from around the British Isles suggest that, as for Northeast Atlantic mackerel (*Scomber*

scombrus), the largest fish tend to travel farthest and may reach areas around the Shetland Islands, the Norwegian coast, and the northern North Sea by September (Eaton, 1983). The population dynamics of western horse mackerel are characterized by sporadic strong year classes, with the very strong 1982 year class constituting the bulk of catches from the mid-1980s to well into the 1990s (Figure 2). This feature is also found in other horse mackerel stocks, such as South African horse mackerel (*Trachurus t. capensis*), which produced two very large year classes that dominated the fishery during the period 1950–1971 (Geldenhuys, 1973), and horse mackerel in the Black Sea (*Trachurus mediterraneus*), which appears to have had highly variable recruitment characterized by sporadic strong year classes (Daskalov, 1999). For western horse mackerel, the strong 1982 year class continued to dominate catches even after it became part of the 11+ age group. Its appearance in the eastern part of the North Sea during the latter half of 1987 led to the development of a sizeable Norwegian fishery for horse mackerel in the late 1980s (ICES, 2008a). More recently, the 2001 year class appears to have been strong, although not as strong as the 1982 year class. Based on catch numbers-at-age (Figure 2), the 1982 year class constituted 75% of the catch on average over ages 3–6 (365 000 t were caught of these ages), whereas the 2001 year class yielded just 42% (207 000 t).

The fishery on western horse mackerel (Figure 1; ICES, 2003; Roel and De Oliveira, 2007) is characterized by the spatial

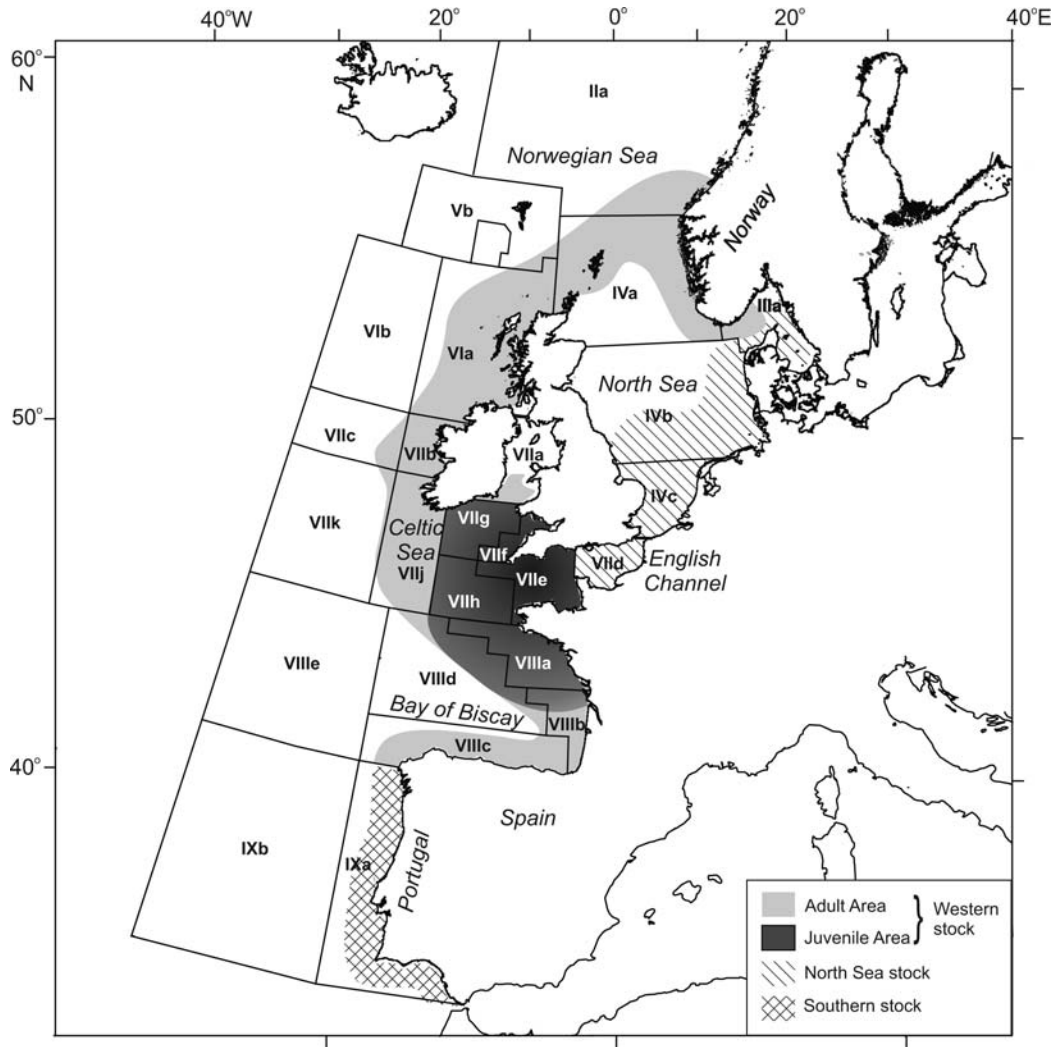


Figure 1. Distribution of horse mackerel in the Northeast Atlantic using the stock definitions of ICES (2005) for the three stocks: western, North Sea, and southern. Note that “adult” and “juvenile” areas are distinguished only for the western stock.

separation of one component exploiting mainly juveniles (ICES Divisions VIIe, f, g, h, and VIIIa, b, d) and another exploiting mainly adults (ICES Divisions IIa, IIIa-west, IVa, VIa, b, and VIIb, c, j, k). Since the mid-1990s, exploitation has shifted towards juveniles because of the scarcity of older fish (coincident with the demise of the 1982 year class) and the development of a market for juvenile fish. This is evidenced by a gradual increase in the percentage of the total catch (by weight) in the juvenile area from ~40% in 1997 to around 65% in 2003, with a decrease again to <50% in recent years (ICES, 2007). Most of the increase was before 2002, the year that the relatively strong 2001 year class first entered the fishery (Figure 2), and some of the subsequent decrease can be explained by this year class leaving the juvenile area.

Currently, the only fishery-independent data used for the assessment of western horse mackerel are estimates of total annual egg production derived from triennial egg surveys using the annual egg production method (ICES, 2008a, b). The method uses total fecundity (the mean number of eggs that will be produced during the spawning season per unit weight of female) to convert estimated total egg production during the

spawning season into spawning-stock biomass (SSB). Total fecundity is estimated by counting the total number of eggs above a certain size threshold in individual fish over a length range before spawning. The threshold is the size at which eggs undergo vitellogenesis (the process of yolk deposition). It is assumed that all these eggs will be spawned. There are two possible sources of error for this calculation of total fecundity before spawning: (i) atresia—some of the eggs are resorbed during the spawning season, thereby reducing fecundity, and (ii) *de novo* vitellogenesis—some pre-vitellogenic oocytes may become vitellogenic after spawning has commenced, thereby increasing fecundity (Eltink, 1991). The conversion of total annual egg production to SSB was abandoned in 2002 when fecundity increased throughout the spawning season, indicating appreciable levels of *de novo* vitellogenesis (Abaunza *et al.*, 2003; ICES, 2003). This finding, together with observations of relatively low levels of atresia, suggested that western horse mackerel were indeterminate spawners, hence questioning the estimates of total fecundity previously used in the conversions to SSB (ICES, 2003). Stock assessments since 2002 have, therefore, treated estimates of total annual egg production as relative indices of SSB (ICES, 2003; De Oliveira *et al.*, 2006).

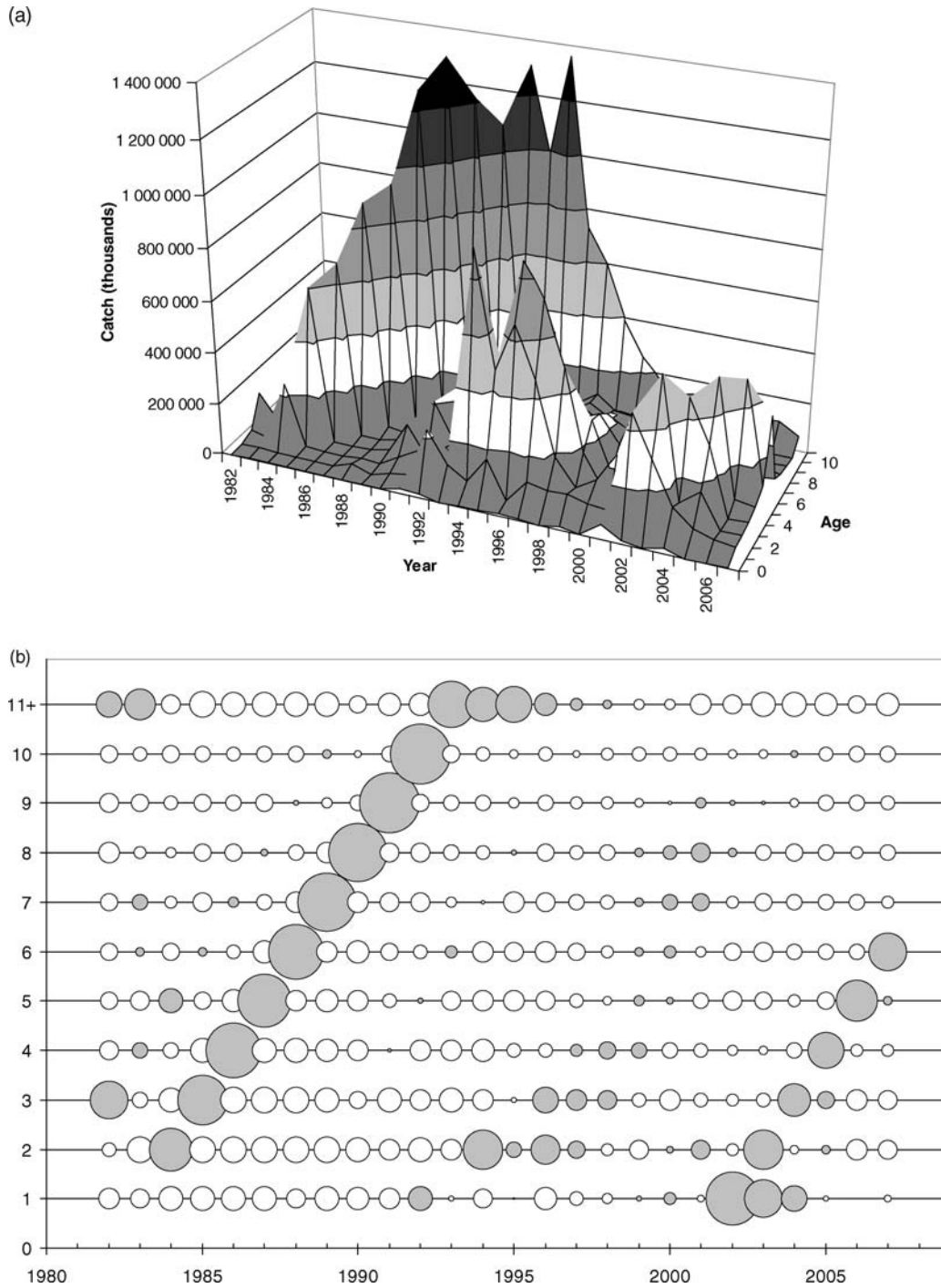


Figure 2. Catch-at-age matrix for western horse mackerel expressed as (a) absolute numbers, and (b) as proportions-at-age, standardized for each age by subtracting the mean and dividing by the standard deviation over the time-series for that age. The grey bubbles in (b) indicate positive values, and the white ones negative values (note that age 11 is a plus-group).

There is evidence that potential fecundity, the number of vitellogenic eggs before spawning per female mass unit (kg), increases with fish weight (ICES, 2002). Realized fecundity per kg, defined as potential fecundity corrected for atretic losses and *de novo* vitellogenesis, is expected to follow the same pattern (P. R. Witthames, pers. comm.). When calculated for the population as a whole (by calculating a weighted mean using mature numbers-at-age), realized fecundity per kg can, therefore, be

expected to depend on the age structure of the population, where a dominance of older, heavier fish would lead to a higher realized fecundity. This is expected to have transpired for the 1982 year class, with realized fecundity per kg for western horse mackerel increasing as the cohort aged and gained weight, but decreasing again as the year class diminished. Ignoring this effect in a stock assessment could lead to biased population estimates.

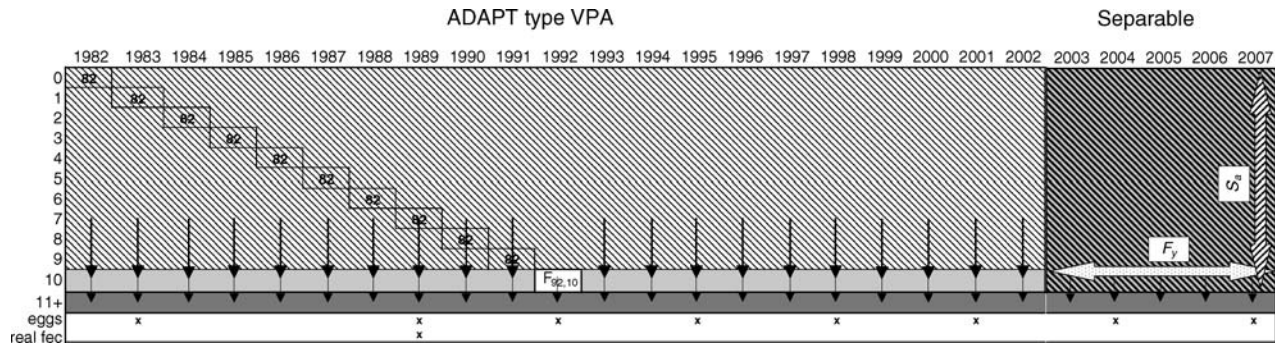


Figure 3. Visualization of the SAD model. For data up to 2002, the model uses an ADAPT VPA formulation, applying a scaling factor F_{scal} to the average fishing mortality for ages 7–9 to obtain fishing mortality at age 10, $F_{y,10}$. However, $F_{92,10}$ is treated as an estimable parameter because of the unique features of the 1982 year class. For data from 2003 on, the model imposes a separable assumption ($F_{y,a} = F_y S_a$). Always, the fishing mortality of the plus-group (11+) is equated to that at age 10. The crosses indicate the years for which egg and realized fecundity data are available. Potential fecundity data (not shown) are also included in the model.

Any stock-assessment method for western horse mackerel needs to be tailored to the particular population dynamics and available data for the stock. As well as providing unbiased estimates for population parameters, it should allow for a fishery developing on the strength of the large 1982 year class, a shift in exploitation towards juveniles in recent years, total annual egg production estimates every third year as the only index available for calibration, and fecundity per kg (potential and realized) as a function of fish weight. In response to the first three of these requirements, a linked separable–ADAPT VPA assessment (SAD) model was developed and applied to western horse mackerel for the first time in 2000 (ICES, 2001). The approach was a modification of the ICA assessment model developed by Patterson and Melvin (1996), in which a separable model is applied to recent data and linked to a VPA transformation of historical catches. Here, we present recent developments of the SAD model that take into account all four features described above, including the incorporation of data on both potential fecundity per kg as a function of fish weight and realized fecundity per kg, to help scale the model. Several model fits to the available data for western horse mackerel are presented. Simulations were also conducted to explore the performance of the model under a variety of scenarios, including trends in fecundity over time.

Material and methods

SAD model description

Data available for conducting an age-structured stock assessment of western horse mackerel are catch- and mean weight-at-age for the period 1982–2007 for ages 0–10 and 11+, total annual egg production estimates for the years 1983, 1989, and every third year until 2007, potential fecundity per kg vs. fish weight for a number of years (219 datapoints spanning the period 1987–2001), and a single “observation” of realized fecundity per kg, with an associated CV, for 1989 (more detail is given below; ICES, 2008a). Natural mortality is assumed to be constant at 0.15 year^{-1} for all ages and years. Maturity-at-age is a fixed input vector that varies by year for the period 1982–1986, but is year-invariant for the years 1987–1997 and 1998–2007, with the latter period reflecting a more sudden change in maturity (age 2 = 5%, age 3 = 25%, age 4 = 70%, age 5 = 95%, age 6 = 100%) than the period immediately preceding it (age 2 = 10%, age 3 = 40%, age 4 = 60%, age 5 = 80%, age 6 = 100%; ICES,

2008a). The model is sex-aggregated, and it is assumed that 45% of the natural and fishing mortality for the year takes place before spawning.

The lack of age-disaggregated information that could be used for model calibration by age-independent catchability estimates implies that an assumption of constant selection-at-age, at least for the most recent years, is required to ensure model identifiability. However, the selective nature of the fishery on the abundant 1982 year class (e.g. the development of the Norwegian fishery in the late 1980s targeting this cohort) and the shift in exploitation towards juveniles in the mid- to late 1990s/early 2000s mean that an assumption of constant selection-at-age is not appropriate before the early 2000s. The SAD model deals with this structural dilemma by coupling a separable VPA (Pope and Shepherd, 1982) for the most recent 5 years (2003–2007) with an ADAPT VPA (Gavaris, 1988) for the rest of the period (1982–2002; Figure 3). The SAD model is similar in structure to ICA (Patterson and Melvin, 1996), but differs through its ability to account for directed fishing on the strong 1982 year class, even after it entered the plus-group.

The separable period assumes constant selection-at-age, requiring estimation of a fishing mortality year (F_y ; $y = 2003, \dots, 2007$) and age (S_a ; $a = 1, \dots, 10$) effect, such that F -at-age is a multiplicative combination of these ($F_{y,a} = F_y S_a$). These estimates are used together with catch-at-age data to calculate population and catch numbers-at-age using the approach described in Pope and Shepherd [1982; Equations (10)–(12) in that paper]. Population numbers from the first year of the separable period are then used to initiate a VPA for the pre-separable period using Pope’s (1972) approximation. Fishing mortality at age 10 in the pre-separable period, $F_{y,10}$, is calculated as the product of the average fishing mortality for the three preceding ages (7–9) in the same year, and a scaling factor F_{scal} , omitting the 1982 year class from these calculations. F_{scal} allows for directed fishing of larger fish at the oldest ages, so accommodating directed fishing of the 1982 year class, which continued to dominate catches even after it entered the plus-group. An independent fishing mortality parameter at age 10, $F_{92,10}$, accommodates directed fishing on the 1982 year class before it enters the plus-group.

For the plus-group in both the separable and pre-separable periods, F is set equal to that at age 10, and population numbers are aggregated [Equation (5) of Deriso *et al.*, 1989]. This

aggregation, combined with the assumption of $F_{y,11+} = F_{y,10}$, allows catches in the plus-group to be estimated, which in turn allows an additional term to be included in the likelihood for plus-group catches. This approach requires population numbers in the plus-group of the first year (1982) to be calculated from the plus-group catch of that year using the Baranov catch equation [Equation (1.22) in Quinn and Deriso, 1999], so that there is no plus-group residual for that year.

The SAD model explicitly incorporates and directly fits potential and realized fecundity data, with separate parameters for the two types of fecundity, so placing the estimation of fecundity parameters in a self-consistent framework instead of deriving them externally to the model. The realized fecundity “observation” and associated CV (1.847 million eggs kg^{-1} of spawning female, $CV = 0.287$) is derived from a normal distribution, in log-space, which covers (with 95% probability) the range of realized fecundity values for horse mackerel reported by Abaunza et al. (2003), i.e. 1.040–3.280 million eggs kg^{-1} of spawning female. This formulation is similar to placing a Bayesian prior on the realized fecundity estimate and allows the incorporation of a level of uncertainty about realized fecundity that is consistent with the range of published values. Although the data used to formulate the prior were collected over a number of years and for several stocks of horse mackerel, including western horse mackerel (Abaunza et al., 2003), the data associated with the western horse mackerel stock were collected during a dedicated survey in 1989 for the application of the daily egg production method (Eltink, 1991), so that year is used in the model fit for realized fecundity.

The model estimates egg production as follows:

$$\hat{N}_{\text{egg},y} = \sum_i q_{\text{fec}}(a_{\text{fec}} + b_{\text{fec}}w_{y,i}) B_{y,i}^{\text{SP}} s^f, \quad (1)$$

where i represents the age, y the year, q_{fec} the realized fecundity parameter, a_{fec} and b_{fec} the potential fecundity parameters, $w_{y,i}$ the mean weights-at-age in the population, $B_{y,i}^{\text{SP}}$ the SSB-at-age calculated by projecting the population to spawning time and accounting for fishing and natural mortality before spawning, and s^f is the female sex ratio, assumed to be 0.5.

Potential fecundity kg^{-1} of spawning female is estimated as

$$\hat{f}_{y,j}^p = a_{\text{fec}} + b_{\text{fec}}w_{y,j}, \quad (2)$$

where $w_{y,j}$ are the sample weights for sample j of year y associated with the potential fecundity data $f_{y,j}^p$, and a_{fec} and b_{fec} are as above. The potential fecundity data were collected during the triennial egg surveys designed to implement the annual egg-production method and from additional fish collections (ICES, 2002). Realized fecundity kg^{-1} of spawning female for the population as a whole is estimated from

$$\hat{f}_y^r = \frac{q_{\text{fec}}}{\sum_i N_{y,i} m_{y,i}} \sum_i N_{y,i} m_{y,i} (a_{\text{fec}} + b_{\text{fec}}w_{y,i}), \quad (3)$$

where i represents the age, y the year, $N_{y,i}$ the population numbers-at-age, $w_{y,i}$ the mean weights-at-age in the population, $m_{y,i}$ the maturity-at-age, and q_{fec} , a_{fec} , and b_{fec} are as above.

The likelihood function, expressed as a negative log-likelihood, contains several components of data:

$$\begin{aligned} -\ln L = & \frac{1}{2} \sum_{y \in Y_{\text{egg}}} \left\{ \frac{(\ln N_{\text{egg},y} - \ln \hat{N}_{\text{egg},y})^2}{\hat{\sigma}_{\text{egg}}^2} + \ln[2\pi\hat{\sigma}_{\text{egg}}^2] \right\} \\ & + \frac{1}{2} \sum_{y=2003}^{2007} \sum_{i=1}^{10} \left\{ \frac{(\ln C_{y,i} - \ln \hat{C}_{y,i})^2}{\hat{\sigma}_{\text{sep}}^2} + \ln[2\pi\hat{\sigma}_{\text{sep}}^2] \right\} \\ & + \frac{1}{2} \sum_{y=1983}^{2007} \left\{ \frac{(\ln C_{y,11+} - \ln \hat{C}_{y,11+})^2}{\hat{\sigma}_{11+}^2} + \ln[2\pi\hat{\sigma}_{11+}^2] \right\} \\ & + \frac{1}{2} \sum_{y \in Y_{\text{pfec}}} \sum_{j=1}^{J_y} \left\{ \frac{(\ln f_{y,j}^p - \ln \hat{f}_{y,j}^p)^2}{\hat{\sigma}_{\text{pfec}}^2} + \ln[2\pi\hat{\sigma}_{\text{pfec}}^2] \right\} \\ & + \frac{1}{2} \left\{ \frac{(\ln \bar{f}_{1989}^r - \ln \hat{f}_{1989}^r)^2}{\sigma_{\text{rfec}}^2} + \ln[2\pi\sigma_{\text{rfec}}^2] \right\}, \quad (4) \end{aligned}$$

where i represents the age, y the year, $N_{\text{egg},y}$ the total annual egg-production estimates, $C_{y,i}$ the catch-at-age by number, $f_{y,j}^p$ the potential fecundity per kg for sample j in year y , and \bar{f}_{1989}^r the realized fecundity per kg for 1989. Model estimates are shown with “ \wedge ”. Y_{egg} and Y_{pfec} represent the years for which, respectively, egg and potential fecundity data are available.

The estimable parameters are as follows: (i) fishing mortality year effects (F_y) for the separable period; (ii) fishing mortality age effects (S_a , the selectivities) for ages 1–10 (excluding age 8, which is set at 1); (iii) the scaling parameter (F_{scal}) for fishing mortality at age 10 relative to the average for ages 7–9 (ignoring the 1982 year class, where appropriate); (iv) fishing mortality on the 1982 year class at age 10 in 1992 ($F_{92,10}$); (v) realized fecundity parameter (q_{fec}), relating potential fecundity to realized fecundity, and also SSB to egg production; and (vi) potential fecundity parameters (a_{fec} and b_{fec}), relating potential fecundity per kg to fish weight.

The model is programmed in AD Model Builder (Anon., 2009), and the estimates of precision are obtained using Hessian-based approximations (combined with the Delta method for quantities that are functions of estimable parameters).

Simulation tests

Simulation tests were conducted in two phases using the scheme described by Wang et al. (2005, their Section 2.2), which was designed to evaluate the performance of stock-assessment methods using simulation. Pseudo-data were generated differently for each phase.

The first phase was used to check if the SAD model could reproduce population estimates given the estimated levels of observation error. During this phase, the SAD model was fitted to available data for western horse mackerel. This initial fit provided the “true” population values, which were then used to generate 100 sets of pseudo-data with levels of observation error estimated from the initial fit, i.e. for j th pseudo-data realization of Z , $Z_j = \hat{Z}e^{\varepsilon_j}$, where $\varepsilon_j \sim N[0; \hat{\sigma}_Z^2]$ and \hat{Z} and $\hat{\sigma}_Z^2$ represent estimates from the initial fit, as shown in Equation (4). The single set of true population values could then be compared with the 100 sets of estimated population values by refitting the SAD model to the pseudo-datasets. Relative error was calculated as $(\hat{x}_j - x)/x$,

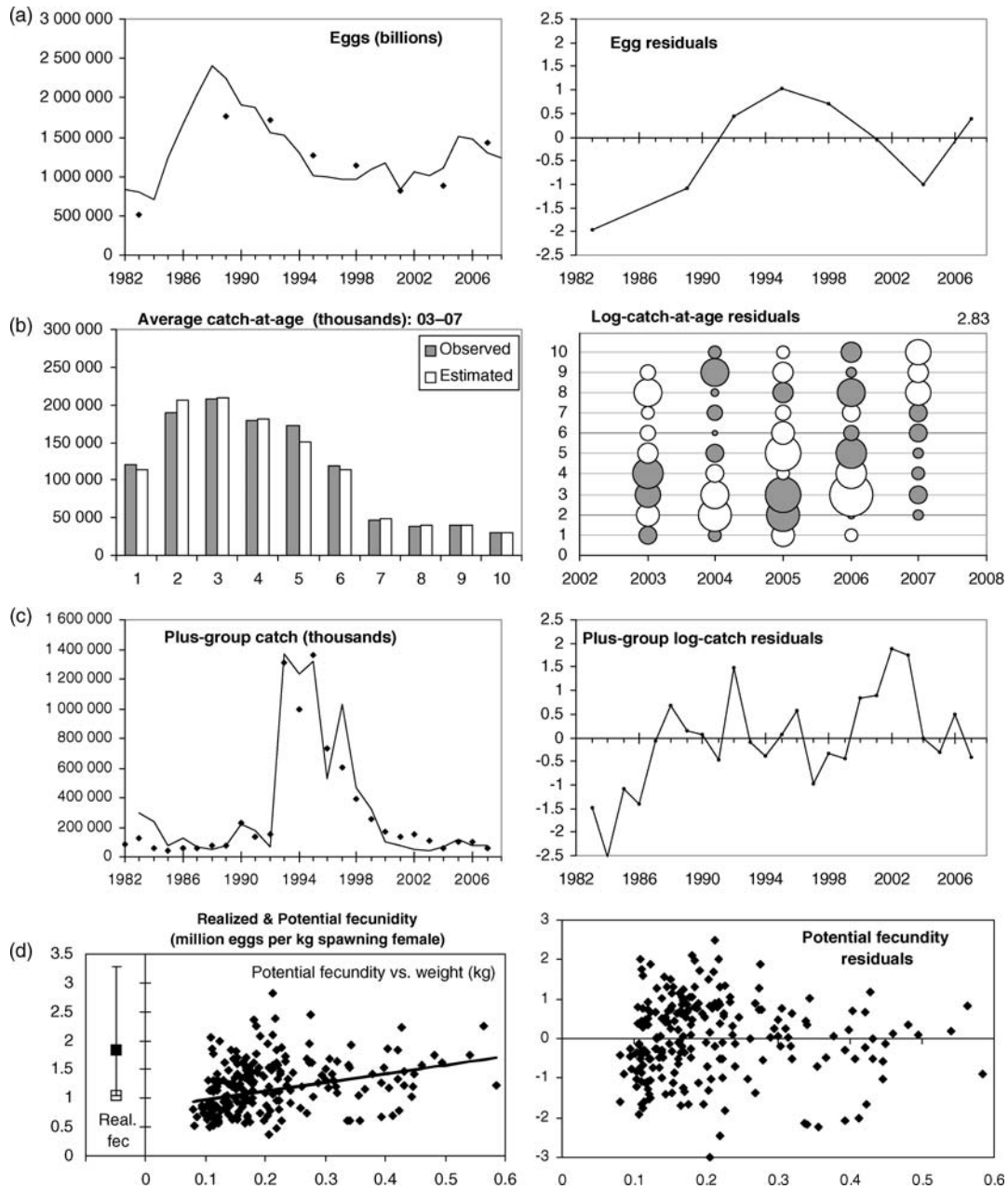


Figure 4. Model fits to data for the five components of the likelihood, corresponding to (a) total annual egg production estimates, (b) catches in the separable period, (c) catches in the plus group, and (d) realized fecundity (left of y -axis, the error bars indicating ± 2 s.d., transformed from log-space), and potential fecundity (right of y -axis). The left column of plots shows the actual fit to the data [average catches are shown in (b) for ease of presentation], and the right column the normalized residuals of the form $(\ln X - \ln \hat{X})/\sigma$. In the residual plot for (b), grey bubbles represent positive residuals, and the area of a bubble reflects the size of the residual, with the maximum absolute size given at the top right of the plot. In the residual plot for (d), only the potential fecundity residuals are shown (there is only one residual for realized fecundity). Apart from in (b), observations in the left column of plots are shown as solid symbols.

where x represents the true population estimate and \hat{x}_j the estimate from a fit to pseudo-dataset j .

The second phase involved the construction of an operating model outside the SAD model, with some of the features of the western horse mackerel stock (such as the large recruitment in 1982), but not directly based on the data for the stock. The intention was to evaluate the SAD model against datasets with different characteristics. Four operating models were constructed with the

following features: (i) low- F scenario (0.05 year^{-1}); (ii) high- F scenario (0.4 year^{-1}); (iii) positive trend in the realized fecundity parameter of 2% per year; and (iv) a realized fecundity parameter that varied randomly over time ($CV = 0.3$).

These scenarios were selected to explore model performance given a population that is exploited at different levels of intensity, and given trends and variability in the realized fecundity parameter. Trends in realized fecundity have been noted for

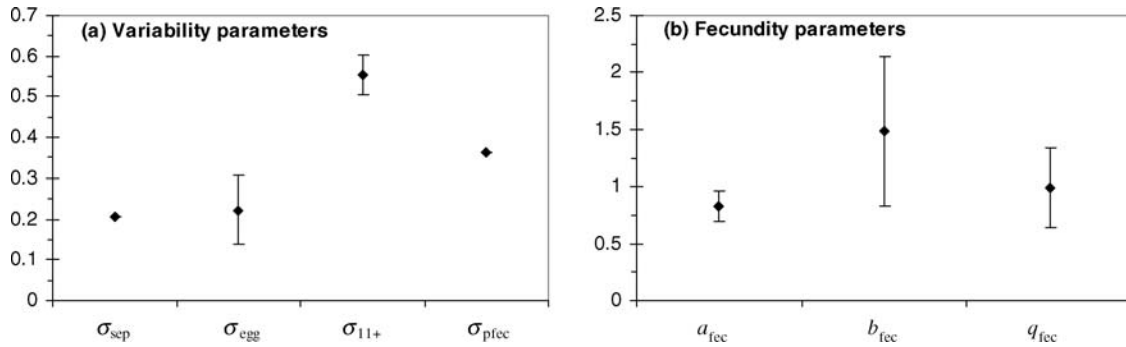


Figure 5. Estimates for some key parameters, (a) corresponding to variability parameters, plotted as standard deviations, for four components of the likelihood (σ_{sep} , σ_{egg} , σ_{11+} , and σ_{pfec}), and (b) fecundity parameters a_{fec} , b_{fec} , and q_{fec} . The error bars are 2 s.d. (indicating roughly 95% confidence bounds).

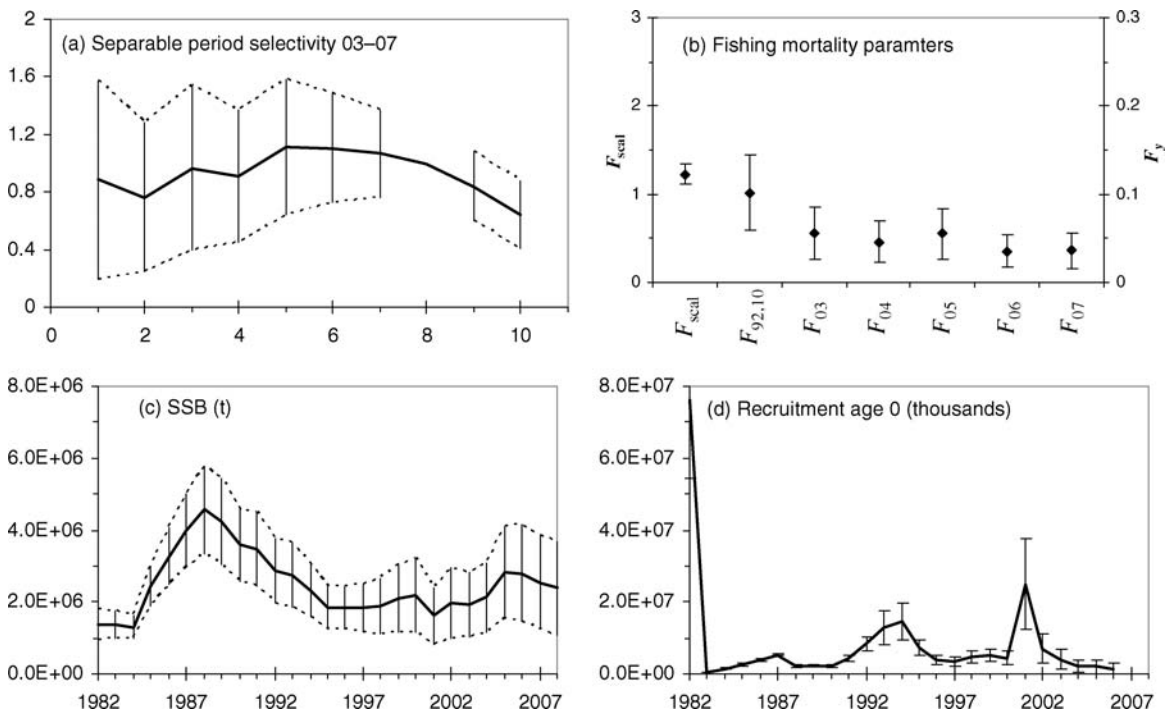


Figure 6. Plots of (a) selectivity pattern, (b) fishing mortality parameters (the scaling parameter F_{scal} , fishing mortality at age 10 in 1992, $F_{92,10}$, and fishing mortality year effects for the separable period, F_y), (c) SSB trajectory, and (d) recruitment at age 0. The error bars are 2 s.d. (indicating roughly 95% confidence bounds).

Northeast Atlantic mackerel (Figure 2.5.3.1 of ICES, 2004). Unlike the first phase, operating models in the second phase produce 100 sets of “true” values, from each of which is produced a set of pseudo-data, so the relative error becomes $(\hat{x}_j - x_j)/x_j$ for the j th set of each operating model, where x_j represents the true population estimate from the j th set of true values, and \hat{x}_j the estimate from a fit to the corresponding j th set of pseudo-data.

Results

Fits to western horse mackerel data

Model fits to the western horse mackerel data based on each of the components of the likelihood function [Equation (4)] are summarized as standard output plots (Figure 4). The normalized residual plots (right column) show no obvious model misspecification, apart from a trend for the earliest years for the plus-group

catch (Figure 4c). This is caused by assuming a common scaling parameter (F_{scal}) for all years in the pre-separable period, indicating that there was no increased targeting of the plus-group relative to younger age groups during these early years. Nonetheless, the fit to the remainder of the plus-group catch is good, and the general trends in the plus-group catch are followed, particularly the influx of the large 1982 year class. Although the fit in the separable period to catch-at-age in individual years varies somewhat (log catch-at-age residuals for Figure 4b), the overall effect is a close fit to the average catch-at-age over the separable period. The realized fecundity estimate favours the values towards the lower end of the range of published values (Figure 4d, left of the y -axis), so leading to the estimates of a higher stock size [Equations (1)–(4)], and hence the lower values of F for the western horse mackerel stock. A sensitivity test (not shown) omitting the realized

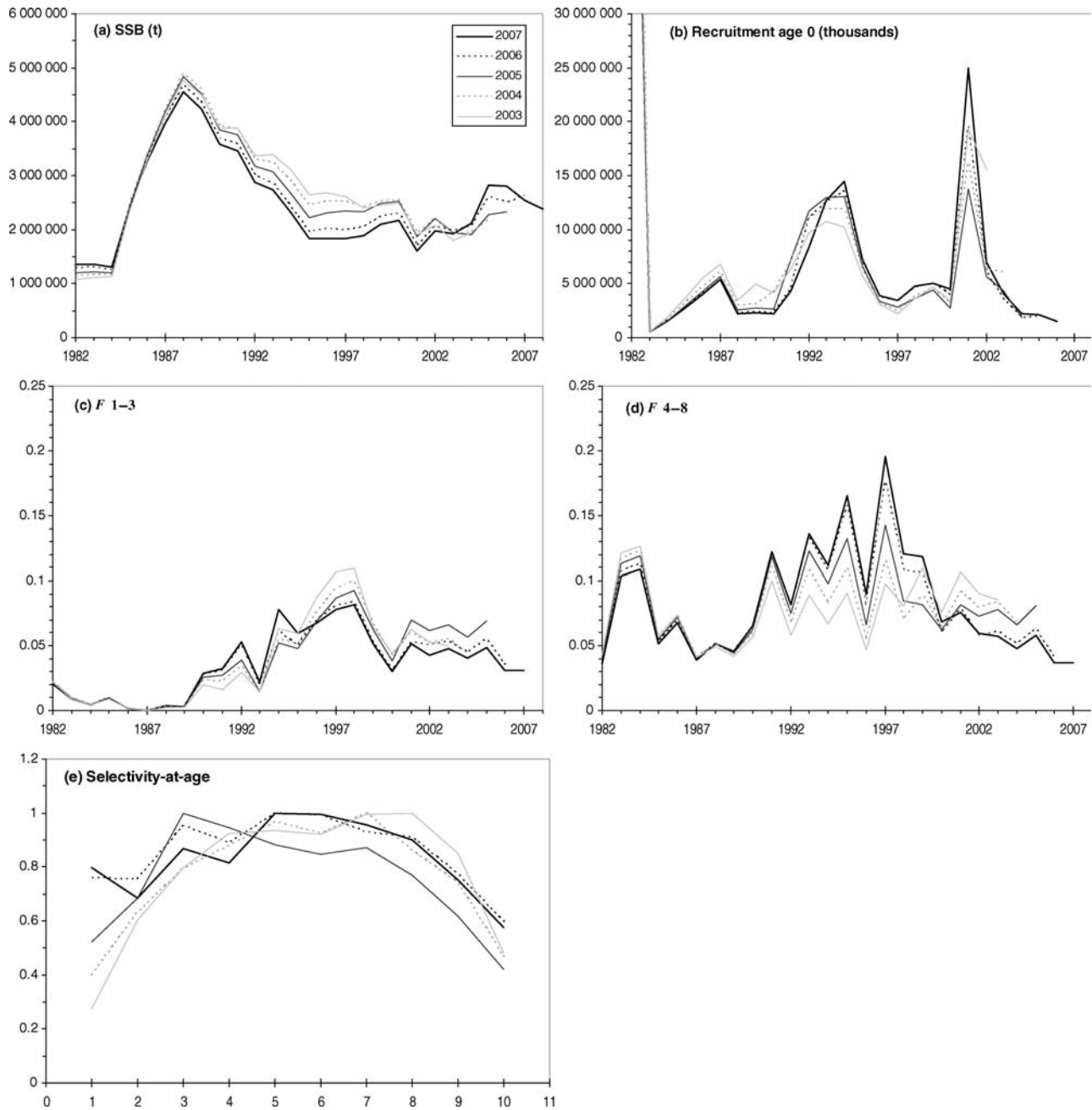


Figure 7. Five-year retrospective plots, where the length of the separable window is kept at 5 years. Trajectories of SSB, recruitment (age 0), F_{1-3} , and F_{4-8} are shown in plots (a)–(d), and plot (e) shows selectivity-at-age, normalized so that the maximum value for each curve is 1. F_{x-y} in plots (c) and (d) indicates the average fishing mortality over ages $x-y$.

fecundity component of the likelihood led to even higher estimates of stock size (SSB estimates $\sim 30\%$ higher on average), indicating that information on realized fecundity helps to scale the model.

There were no strong correlations among estimable parameters, except where these were to be expected because of the model structure (such as among the separable period fishing mortality F_y and selectivity S_a parameters, and between the scaling parameter q_{fec} and the fishing mortality parameters). Estimates of the variability parameters associated with each component of the likelihood, apart from that associated with realized fecundity, which is a fixed input [Equation (4)], are shown in Figure 5a. The plus-group

and potential fecundity data are the most variable, with σ values of 0.55 and 0.36, respectively, and the values for the egg production and separable period catch-at-age data are ~ 0.2 . The σ -values are precisely estimated for the potential fecundity and separable period catch-at-age data because of the quantity of data used (219 datapoints for the former, 50 for the latter). Estimates for the fecundity parameters, given in Figure 5b, show that the relationship between potential fecundity per kg of spawning female and weight [Equation (2)] has a slope significantly different from zero (the 95% confidence bound of b_{fec} does not include zero). This indicates that potential fecundity, and therefore

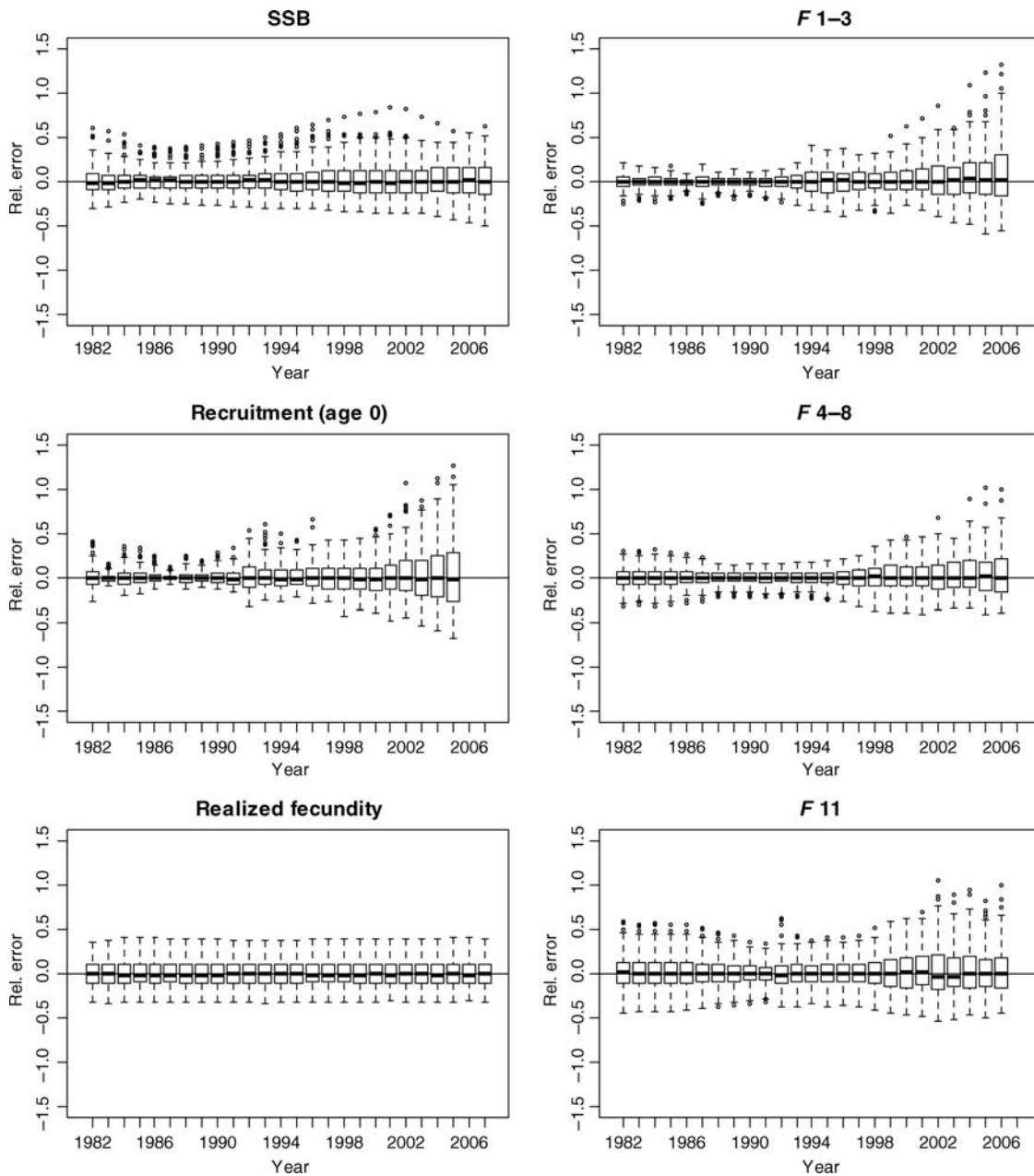


Figure 8. Box-and-whisker plots showing relative error for the quantities indicated for phase 1, where pseudo-data are generated by the SAD model based on fits to actual data up to 2006 (but including the 2007 egg production estimate), and subsequently fitted with the SAD model. Relative error is calculated as $(\hat{x} - x)/x$ (with “^” indicating model estimates, and without “^” indicating the “true” values from which the pseudo-data are generated).

realized fecundity, does change with fish weight, so the relationship should be accounted for when estimating egg production [Equation (1)]. On the other hand, the parameter linking potential and realized fecundity, q_{fec} , is estimated at 0.99, with 95% confidence bounds (0.64–1.34), covering the value 1 and implying that the effects of *de novo* vitellogenesis and atresia, on average, cancel each other out for western horse mackerel.

For the younger ages, the selectivity-at-age curve precision in the separable period is low, improving from 40% at age 1 to ~15% at the older ages (Figure 6a). Selectivity is relatively flat for all ages in the separable period apart from the oldest ages,

when it appears to decline, with selectivity at age 10 significantly < 1 (the value assumed for age 8). This is in contrast to the pre-separable period estimate of the scaling parameter F_{scal} , with an estimate only just more than 1 (1.23), but with 95% confidence bounds that exclude 1 (Figure 6b), indicating an increase in selectivity at age 10 relative to the average for ages 7–9. The precision of the estimates of SSB and recruitment at age 0 deteriorates with time (Figure 6c and d), with average CVs of 14 and 8% for the first half of the series, respectively, compared with 22 and 26% for the second half. The shape of the SSB trajectory is similar to that for annual egg production because realized fecundity is

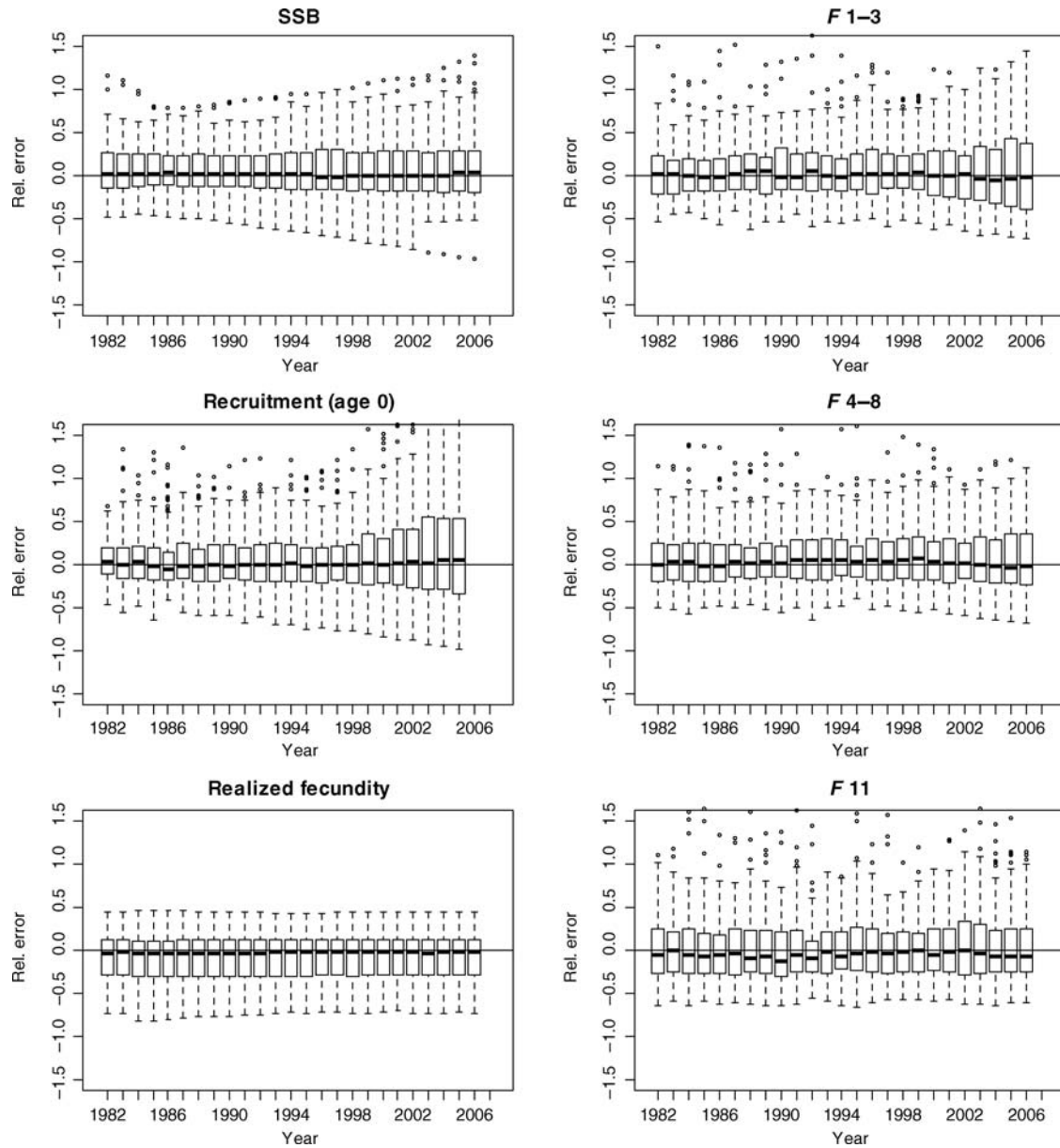


Figure 9. Box-and-whisker plots showing relative error for the quantities indicated for phase 2, where pseudo-data are generated by operating model (a) with low F (0.05 year^{-1}), and subsequently fitted with the SAD model. See Figure 8 legend for more detail.

relatively flat (point estimates varying between 0.98 and 1.12 million eggs kg^{-1} of spawning female). Estimates of fishing mortality are low, $\sim 0.05 \text{ year}^{-1}$ during the separable period (Figure 6b).

Estimating $F_{92,10}$ instead of assuming it to be the average of the three preceding ages multiplied by F_{scal} , as is assumed for the other $F_{y,10}$ values in the pre-separable period, leads to a significant improvement in model fit. A comparison of AIC_c values (Burnham and Anderson, 2002) shows an improvement from 257 to 247 when $F_{92,10}$ is estimated (results for assuming $F_{92,10}$ to be a scaled average instead of estimating it are not shown). A sensitivity test imposing an independent multiplicative factor on F applied to the large 2001 year class during the separable period (so introducing an additional parameter; results not shown) did not lead to a significant improvement in model fit,

implying that the 2001 year class was not targeted in the same manner as the 1982 year class.

Retrospective plots of population trends were constructed by first fitting the model to all data (“2007”), then removing 2007 data, moving the separable window 1 year back while keeping its length at 5 years, and fitting the model to the truncated dataset (“2006”), and so forth (Figure 7). The plots indicate retrospective bias throughout the time-series for SSB, recruitment, and F , with changes in the bias from one direction to the other, and back again. This behaviour is likely because of changes in selectivity-at-age for the separable period as the window is moved back in time, a change that indicates increasing selection of the younger ages over time (Figure 7e). Retrospective bias in the first two-thirds of the time-series is negligible, but it is still present in the last one-third, when retrospective plots are

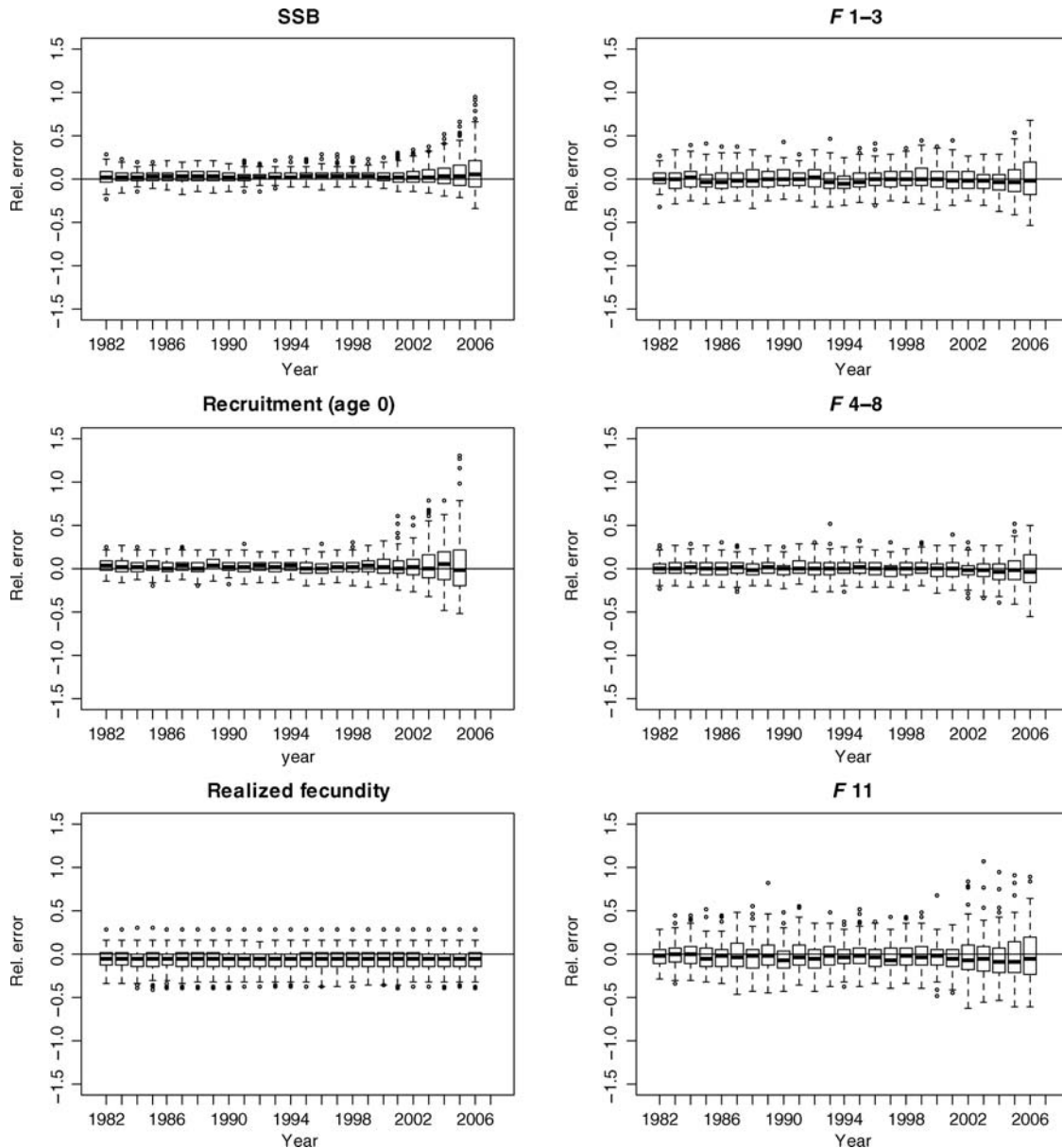


Figure 10. Box-and-whisker plots showing relative error for the quantities indicated for phase 2, where pseudo-data are generated by operating model (b) with high F (0.4 year^{-1}), and subsequently fitted with the SAD model. See Figure 8 legend for more detail.

constructed as above, but the first year of the separable window is fixed at 2003, so the separable window becomes smaller (results not shown). This result supports the interpretation that it is the change in selection before 2003 that causes the retrospective patterns throughout the time-series, as shown in Figure 7.

Simulation tests

The phase 1 simulation test confirms that the SAD model is able to reproduce population estimates without bias, given the estimated levels of observation error in the western horse mackerel data (Figure 8). This provides reassurance that the SAD model is behaving as expected. A further feature of Figure 8 is the increased uncertainty in recent years, reflecting the availability of less information in recent years for estimation, a characteristic typical of these types of model.

Results for the phase 2 simulation tests are plotted in Figures 9–12. The results for operating models (a) and (b), i.e. low- F and high- F scenarios (Figures 9 and 10, respectively), reveal that the SAD model produces unbiased population estimates in both cases. The spread of relative errors is much lower for the high- F scenario than for low F , confirming the long-established fact in fisheries stock assessment that VPA-based methods perform better (i.e. give more precise estimates) in high- F situations than in low F ones (e.g. Figure 1 in Pope, 1972; Lassen and Medley, 2000).

For a temporal trend in realized fecundity [operating model (c); Figure 11], the performance of the SAD model deteriorates markedly, producing positively biased SSB and recruitment estimates, and negatively biased F and realized fecundity estimates. This result is not surprising, given that the SAD model does not

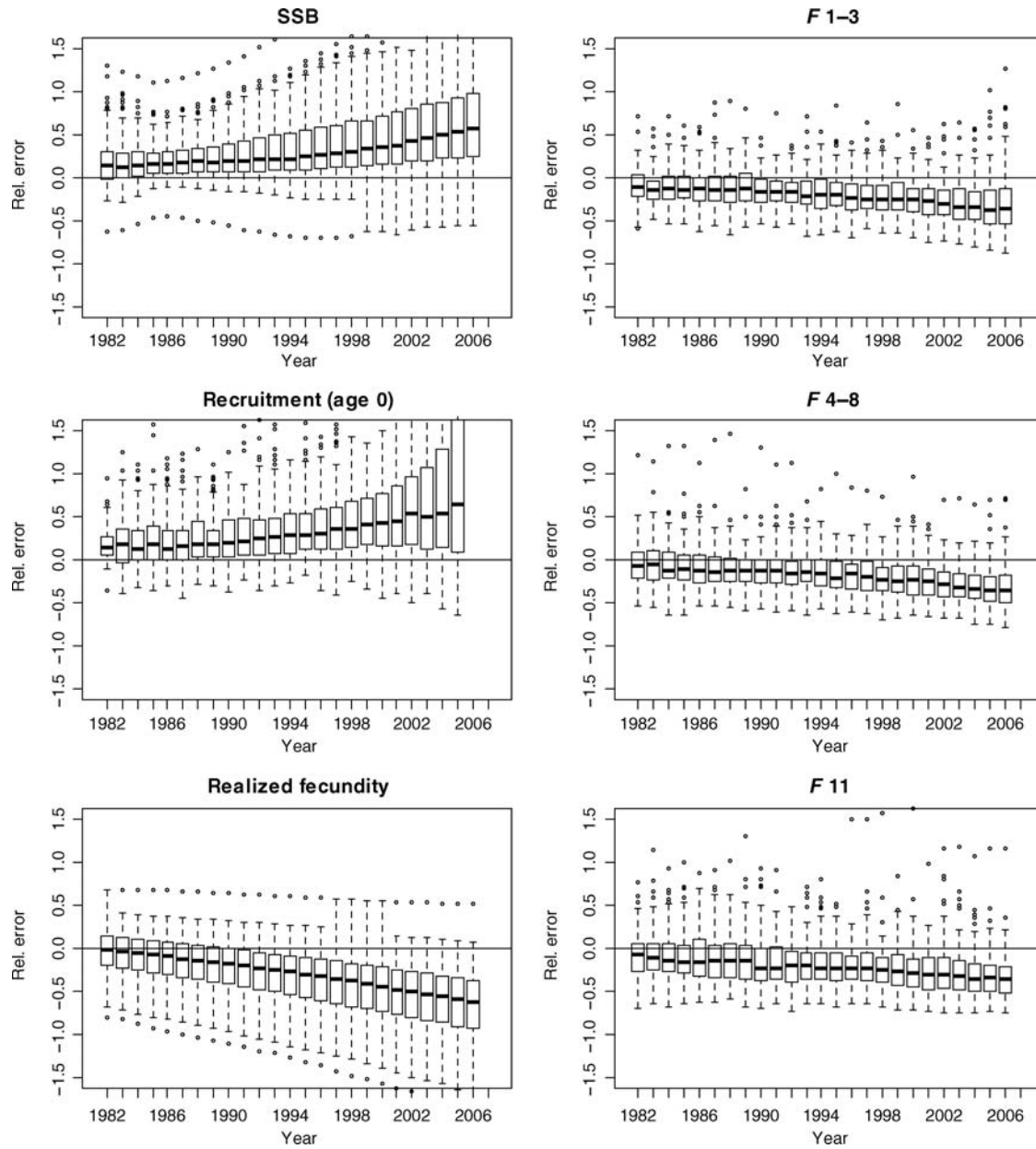


Figure 11. Box-and-whisker plots showing relative error for the quantities indicated for phase 2, where pseudo-data are generated by operating model (c) that has a trend in realized fecundity, with the realized fecundity parameter increasing by 2% per year, and subsequently fitted with the SAD model. See Figure 8 legend for more detail.

account for trends in the realized fecundity parameter q_{fec} (assuming it to be constant over time), so that for operating model (c), model misspecification is present. Performance is also poor for the case where the realized fecundity parameter varies randomly over time [operating model (d); Figure 12], producing large relative errors, but in this case, the interquartile range still includes zero [it did not include zero for operating model (c)].

Discussion

A particular challenge for developing a stock-assessment model for western horse mackerel is dealing with the paucity of data on abundance trends. Although Magnusson and Hilborn (2007) found that the use of total catch and catch-at-age data

on their own (i.e. omitting indices of relative abundance) could provide considerable information on absolute abundance and relative depletion, they also found that combining these data with indices of relative abundance resulted in estimation models performing better. This agrees with the conclusion of Deriso *et al.* (1985) that all three data sources are needed for the reliable estimation of abundance and reference points. It would, therefore, seem appropriate to utilize the egg data on abundance trends, although the data are only available every third year and require additional information on fecundity to be interpretable as indices of abundance. The SAD model aims to achieve this by combining all these sources of data into a single framework.

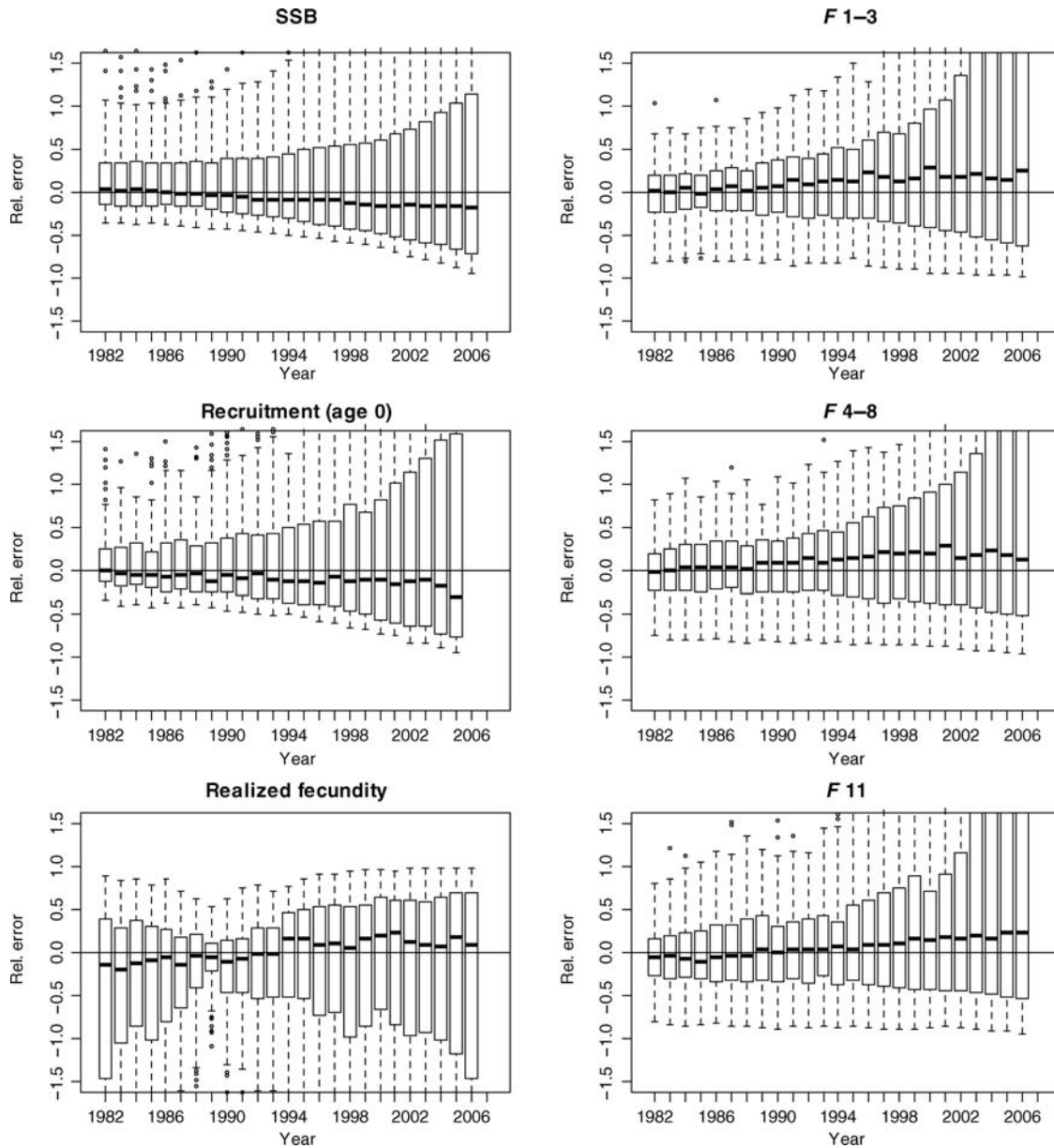


Figure 12. Box-and-whisker plots showing relative error for the quantities indicated for phase 2, where pseudo-data are generated by operating model (d) that has a realized fecundity parameter varying randomly over time ($CV = 0.3$), and subsequently fitted with the SAD model. See Figure 8 legend for more detail.

Another challenge is dealing with directed fishing, which occurred when a sizeable Norwegian fishery developed on the very strong 1982 year class. XSA (Darby and Flatman, 1994; Shepherd, 1999) is currently used for another stock that is characterized by the sporadic occurrence of large year classes, North Sea haddock (*Melanogrammus aeglefinus*; ICES, 2008c). However, XSA utilizes age-disaggregated tuning indices (based on either commercial or scientific survey catch rates) for calibration, which are not available for western horse mackerel. Northeast Atlantic mackerel has data similar to that for western horse mackerel for assessment purposes, including age-aggregated data from triennial egg surveys as the only data available for model calibration, and is modelled using ICA (Patterson and Melvin, 1996). Although some of the design features of ICA are appropriate for western

horse mackerel (e.g. coupling a separable model for recent years to a VPA for earlier years to deal with data paucity and changing selectivity), it is not suitable for western horse mackerel because it cannot account for the directed fishing on the strong 1982 year class, even after it entered the plus-group. The SAD model is similar in structure to ICA, but was designed to accommodate the features specific to western horse mackerel.

Fecundity data show that potential fecundity per kg of spawning female increases with fish weight (Figure 4d), so realized fecundity per kg would depend on the age structure of the population. Biased population estimates could, therefore, result if the fecundity relationship with fish weight is ignored, particularly given the sporadic occurrence of very strong year classes for western horse mackerel that would have a great impact on the

age structure of the population. The use of fecundity data in the SAD model, incorporating a fecundity relationship with fish weight and a prior for realized fecundity, helps account for any size- and age-dependent effects on fecundity and with scaling the model. Ignoring information on realized fecundity leads to higher estimates of population size (SSB estimates 30% higher, on average).

Simulation tests have shown that the SAD model provides unbiased population estimates, under both high- and low- F scenarios, provided there are no temporal trends in the realized fecundity parameter. This is reassuring, given concerns about scaling in earlier versions of the model. Estimates of F are still relatively low (the average for ages 4–8 was 0.1–0.2 year⁻¹ in the 1990s, dropping to ~0.05 year⁻¹ in recent years), but this is not entirely surprising given the persistence of the 1982 year class in the catch data (it continued to dominate the plus-group for several years; Figure 2). Moreover, the model is designed [final term in Equation (4)] so that the realized fecundity parameter, which effectively scales the model, provides an estimate of realized fecundity per kg that is consistent with the range of published values (Figure 4d). The resultant estimate of the realized fecundity parameter is 0.99, with 95% confidence bounds of 0.64 and 1.34, implying that the effects of *de novo* vitellogenesis and atresia tend, on average, to cancel each other out for western horse mackerel.

The SAD model performs poorly in the case where there is a temporal trend in the realized fecundity parameter, and the model does not account for such a trend. Trends in realized fecundity have been noted for Northeast Atlantic mackerel and have been related to variations in food availability (ICES, 2004). If such trends are also a feature for western horse mackerel and are not adjusted for in the SAD model because of a lack of data, they can be expected to introduce bias into the assessment and negatively impact the management of the stock. This highlights the need to improve information on realized fecundity through the collection of appropriate data and, where this is not possible, to develop management plans that are robust to this source of uncertainty (e.g. Roel and De Oliveira, 2007).

In conclusion, the SAD model makes the best use of the limited available data by producing fits with no obvious model misspecification, with simulation tests indicating that, in the absence of temporal trends in the realized fecundity parameter, the model produces unbiased population estimates. It also makes use of combinations of data that are not commonly used in stock assessments (e.g. potential and realized fecundity data), because of the need to overcome the paucity of data for western horse mackerel. The model in its current form is very specific to the western horse mackerel stock, but its construction (based on a likelihood function fitting to various components of data) makes it similar to models such as stock synthesis (Methot, 1990), where the inclusion of different types of data and modifications to effect such inclusions are possible. The application of a suitably modified SAD model to other stocks with similar data availability and features to western horse mackerel is, therefore, possible.

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