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Investigating the Use of Proxies for Fecundity to Improve the Management of Western Horse Mackerel

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Observations of fecundity from the most recent Western horse mackerel spawning stock biomass survey suggest that the species is an indeterminate spawner and therefore the current model of fecundity, used in the calibration of the stock assessment, may be inappropriate. The stock is assessed by fitting a linked Separable and ADAPT VPA-based model to the catch-at-age data and to the egg production estimates. The assumption is made that egg production and spawning stock biomass are linked by a constant but unknown fecundity parameter, estimated within the model. In this study, the sensitivity of the model structure to alternative fecundity relationships is explored. The introduction of models linking biological indicators of fecundity, such as lipid content or feeding intensity during the spawning season is examined. The impact on the perception and management of this stock is evaluated within a simulation framework. Simulations suggest that care must be taken when incorporating time series of proxies when the underlying relationships with fecundity are poorly described, weak or based on few data.

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INTRODUCTION

Problems have recently arisen in the assessment of the western horse mackerel stock. For a number of years questions about the spawning strategy of western horse mackerel have been raised, and in 2003 growing evidence led scientists to conclude that it was an indeterminate spawner (ICES 2003a). The only fishery-independent data for calibration of the assessment model is a time-series of triennial egg survey estimates. Prior to 2002, this time series was combined with fecundity estimates to create an SSB time series. However in 2002, given concern about the fecundity estimates, a total egg production time series was used instead (ICES 2003b). Total egg production time series can be used in assessments in the same way as larval abundance series (ICES 2003c), but if large scale trends in fecundity occur (as seen in NE Atlantic mackerel, ICES 2003a; and noted in horse mackerel, Macer 1974; Karlou-Riga and Economidis 1996), they may introduce bias into the assessment and negatively affect the management of the stock. Large variability in short time series will also have an impact on management because the assessment is annual (using annual catch data), but the tuning index (the egg surveys) is triennial (Simmonds pers. comm.).

With this worry in mind, it was proposed that a proxy could be used to account for variability in fecundity (Marshall *et al*. 1999, Blanchard *et al*. 2003). Such a proxy may be condition factor, lipid content or feeding intensity during the spawning season (Schülein *et al*. 1995, Girish and Saidapur 2000; Kreiner *et al*. 2001, Henderson and Morgan 2002). However, it is probable that the assessment will only improve if the predictive power of an index is substantial. Also, to remain biologically competent, it is important to understand the functional relationship between the index of the proxy and fecundity prior to its use.

There are other problems in the assessment of western horse mackerel. The stock has been dominated by a series of strong cohorts with the extremely strong 1982 and the less abundant 1987 year classes constituting the bulk of the recent catches. Additionally, in recent years there has been a change in the selection pattern towards increasing exploitation of younger fish. To account for some of these problems, the stock is now assessed by fitting a linked Separable VPA and ADAPT VPA-based model (SAD; ICES 2003b) to the catch-at-age data and to the egg estimates. An assumption is made that the egg production estimates are based on a constant but unknown fecundity that is estimated in the assessment model.

In this study, we use a simulation framework to investigate the effects of different assumptions about the relationship between an index of fecundity (the proxy) and true fecundity on the sustainable exploitation of the stock. We consider the strength and nature of this relationship within the context of management advice. The underlying stock dynamics assumes three possible functional forms for the relationship between the index and true fecundity, one linear and two non-linear. The exploitation is regulated on the basis of an annual TAC calculated as a fraction (α) of the perceived spawning stock biomass (SSB^{perc}). The consequences of assuming fecundity constant, the current practice, or making use of an index of fecundity with its associated potential problems, are evaluated by simulation.

METHODS

Simulations are based on a deterministic age structured model with recruitment generated on a stochastic basis; these serve as the "true" underlying dynamics of the western horse mackerel stock (Appendix). The stock-recruit function used is a mixture between a Ricker function and a process that overrides the Ricker function to allow for the influx of a very large recruitment roughly once in 20 years. (Macer 1977, Eltink and Kuiter 1989).

Management is based on the perception of the spawning stock biomass (SSB^{perc}), which is obtained from an estimate of egg abundance (the "observed" egg abundance, EGG^{obs}) by either using a fecundity index or not. The fundamental question asked in this simulation study is whether and to what extent the management of the western horse mackerel stock can be improved (in terms of minimising the risk of spawning stock biomass falling below Bpa, and maximising catches) by incorporating a fecundity index to obtain SSB^{perc} (compared to the current practice of not using a fecundity index for SSB^{perc}). In order to investigate this question, a model is required linking SSB^{perc} to the "true" spawning stock biomass, SSB^{true}, through the following chain:

$$\boxed{SSB^{true} \xrightarrow{1} EGG^{true} \xrightarrow{2} EGG^{obs} \xrightarrow{3} SSB^{perc}}$$

Given the underlying process linking EGG^{true} to SSB^{true} (link 1), would the incorporation of the perceived knowledge of this process (link 3) with its associated problems (measurement error, parameter estimation problems, the underlying process in link 1 not properly understood) improve management of the western horse mackerel stock? The method used to investigate this question is similar to that used by De Oliveira and Butterworth (in press) to investigate the incorporation of environmental indices as predictors of recruitment in order to improve management of the South African anchovy stock.

"True" egg abundance:

The "true" egg abundance is modelled on the basis of the relationship between egg abundance and spawning stock biomass estimated from the SAD model (ICES 2003b). The total variance associated with this relationship can be apportioned into a "process" error component (λ_{egg}) linking "true" egg abundance to "true" spawning stock biomass (where fecundity plays a role), and an "observation" error component (cv_{egg}) linking "observed" egg abundance to "true" egg abundance through the sampling CV of egg abundance estimates. The total variance of the egg abundance - spawning stock biomass relationship is therefore $\lambda_{egg}^2 + cv_{egg}^2$. The values used in this study for λ_{egg} and cv_{egg} are 0.6 and 0.3 respectively. These values were selected to reflect a moderate sampling CV for the egg abundance estimates, but more uncertainty (double the "observed" sampling CV) about the process linking egg abundance to spawning stock biomass. These values were not available from the SAD model, because sampling CVs are not available, and because the SAD model is currently not structured to estimate variances as part of the assessment model fit (ICES 2003b).

EGG^{true} is derived from SSB^{true} with process error, as follows.

$$EGG_y^{true} = \frac{1}{q} SSB_y^{true} \, e^{\varepsilon_y} \tag{1}$$

where

$$\begin{aligned} &\varepsilon_y = r \, \lambda_{egg} \, f_i(I_y) + \sqrt{1-r^2} \, \lambda_{egg} \, \eta_y \\ &I_y \sim \mathrm{N}[0;1]; \ \eta_y \sim \mathrm{N}[0;1] \end{aligned} \tag{2}$$

In equations (1) and (2), $1/q$ is the constant of proportionality linking egg abundance to spawning stock biomass, and ε_y models the process error component, λ_{egg}^2, of the total variance of the egg abundance *versus* spawning stock biomass relationship (in log-terms), which could in part be due to variability in fecundity. As fecundity is difficult to measure directly, a proxy for fecundity, represented by $f_i(I_y)$, is used, where f_i is a functional form relating a fecundity index I_y to fecundity. In equation (2), ε_y is structured such that the variance λ_{egg}^2 has a component explained by I_y, namely: $r \, \lambda_{egg} f_i(I_y)$, and an unexplained component: $\sqrt{1-r^2} \, \lambda_{egg} \, \eta_y$. Assuming that λ_{egg}^2 is entirely due to fecundity, the correlation coefficient r^2 relates to the relationship between fecundity and the index I_y and reflects the proportion of variance that is explained by the index, while η_y is an independently generated random variable. A high r^2 value therefore indicates a very strong relationship between fecundity and the fecundity index I_y, which are linked by the function f_i.

For convenience, equation 1 can be re-written as follows, separating the model component from the random noise component.

$$EGG_y^{true} = \frac{1}{q} SSB_y^{true} \times [e^{r\,\lambda_{egg}\,f_i(I_y)}] \times [e^{\sqrt{1-r^2}\,\lambda_{egg}\,\eta_y}] \tag{3}$$

Functional forms for f_i

Three functional forms for the relationship between the index and fecundity are considered, as follows.

Linear: $$f_1(I_y) = I_y \tag{4}$$

Logistic: $$f_2(I_y) = \arctan(2.5\,I_y) \tag{5}$$

Quadratic: $$f_3(I_y) = \frac{1 - I_y^2}{\sqrt{2}} \tag{6}$$

All three f_i functions have the property that $E[f_i(I_y)] = 0$ and $var[f_i(I_y)] = 1$, so that $E[\varepsilon_y] = 0$ and $var[\varepsilon_y] = \lambda_{egg}^2$. The quadratic model f_3 is perhaps unrealistic for a index - fecundity relationship ($f_3(I_y)$ is positive for $I_y^2 < 1$, otherwise it is zero or negative, so that the index behaves in a similar way to temperature, where successful egg incubation, say, is only possible within a narrow temperature window), but it is nevertheless included to provide a greater contrast between the underlying functional form (in this case quadratic) and its perceived form (always assumed linear) for the "estimated index" (see "*Perceived SSB models*" below).

Observed egg abundance

The observed egg abundance is generated from EGG^{true} with observation error as follows.

$$EGG_y^{obs} = EGG_y^{true}\; e^{cv_{egg}\,\omega_y} \tag{7}$$

where $\omega_y \sim N[0;\,1]$ and cv_{egg} represents the sampling CV related to observed egg abundance estimates.

Perceived SSB models:

Three perceived SSB models are considered relating to how SSB^{perc} is derived from EGG^{obs}.

(a) no index

This model omits the use of an index, and assumes a constant linear relationship between egg abundance and SSB.

$$SSB_y^{perc} = q\; EGG_y^{obs} \tag{8}$$

(b) perfect index

This model assumes perfect knowledge about function f_i (i.e. function f_i is known), and assumes no measurement error for the index. It is therefore unrealistic, but is nevertheless shown to indicate the best one could do by incorporating a fecundity index.

$$SSB_y^{perc} = q\; EGG_y^{obs}\; e^{-\rho_I \lambda_{egg} f_i(I_y)} \tag{9}$$

[Note: for $r^2 = 0$, this model is identical to (a).]

(c) estimated index

This model selects amongst several indices (I_y, J_y, K_y), only 1 of which (I_y) is related to fecundity. Selection is done through stepwise regression assuming a linear model (g), with measurement error included for all the indices and ε_y.

$$SSB_y^{perc} = q\; EGG_y^{obs}\; e^{-g(I_y, J_y, K_y)} \tag{10}$$

where

$$g(I_y, J_y, K_y) = \hat{b}_0 + \hat{b}_1 I_y^{merr} + \hat{b}_2 J_y^{merr} + \hat{b}_3 K_y^{merr} \tag{11}$$

with

$$\left.\begin{array}{l} X_y^{merr} = X_y + m\, \upsilon_{X,y} \\ \upsilon_{X,y} \sim \mathrm{N}[0;1];\; X_y \sim \mathrm{N}[0;1] \end{array}\right\} \qquad X = I, J \text{ or } K \tag{12}$$

Measurement error, m, was set at 0.5.

For each simulation run, a new set of parameters $\hat{b}_0, \hat{b}_1, \hat{b}_2$ and $\hat{b}_3$ for the estimated index model were derived prior to the 20-year projection of that simulation run. This was achieved by generating a 10- or 30-year time-series of “data” $\{\varepsilon_y^{merr}; I_y^{merr}; J_y^{merr}; K_y^{merr}\}$ using equations (2) and (12) (with additionally $X = \varepsilon$ in equation (12) to generate ε_y^{merr}), and applying a stepwise regression technique using equation (11) and forward selection, with a p value of less than 5% serving as a criterion for inclusion of a parameter in the model. Therefore, a situation where (incorrectly) $\hat{b}_1 = 0$, and $\hat{b}_{2/3} \neq 0$

is possible. Once a set of parameters for equation (11) have been derived for a simulation run, they are used for the entire duration of the projection period for that simulation run.

Setting the TAC

A simple constant proportion harvesting strategy is used to set the TAC, as follows:

$$TAC_y = \alpha \; SSB_y^{perc} \tag{13}$$

Summary performance statistics

Summary performance statistics are used to compare the overall performance of one perceived SSB model relative to another. Three summary performance statistics are considered as follows.

(i) "Proportion < Bpa" calculates the number of cases (out of 20 years × 500 simulations) for which SSB^{true} is below Bpa = 500 000t.

(ii) "Median Catch" calculates the median catch from 10 000 (=20 years × 500 simulations) catch realisations.

(iii) "Average Catch Variation" calculates the average variation in annual catch C_y as follows

$$\text{Average Catch Variation} = \tfrac{1}{500}\sum_{sim=1}^{500}\left[\frac{\sum_{y=2004}^{2022}\left|C_y - C_{y-1}\right|}{\sum_{y=2004}^{2022} C_y}\right] \tag{14}$$

RESULTS

Results were obtained for the three perceived SSB models: (a) "no index" which corresponds to the current assumptions in the assessment, i.e. constant fecundity, (b) "perfect index", which assumes perfect knowledge of the relationship between the index and fecundity, and (c) "estimated index", where the parameters of the relationship between the index and fecundity are estimated using a linear model (even if the underlying form of the fecundity index - fecundity relationship is non-linear) with measurement error included. Each of the plots shown provide a comparison between these three perceived SSB models, given values for r^2 (the "strength" of the fecundity index - fecundity relationship), the number of years of data used to estimate the parameters for perceived SSB model (c), and the underlying form of the fecundity index - fecundity relationship.

Assuming a linear underlying functional form for the fecundity index - fecundity relationship and the availability of only 10 years of data for estimating parameters for the "estimated index" model, Figure 1 provides a comparison of the three perceived SSB models for three different r^2 values.

Results indicate that under these conditions, the "no index" model outperforms the "estimated index" model for $r^2 = 0.5$ in terms of "Proportion < Bpa" and "Median Catch". Only under conditions of a very strong fecundity index - fecundity relationship will the "estimated index" model do better than the "no index" model in terms of these two summary statistics, and in terms of "Average Catch Variation". As expected, there is no perceptible change in the "no index" model as r^2 changes. This is because it does not use an index, and because the process error structure (equation 2) maintains the same level of variance (and statistical distribution), regardless of the r^2 value and given a linear underlying functional form for the fecundity index - fecundity relationship.

Figure 1 A comparison of the three perceived SSB models (I: no index; II: perfect index; and III: estimated index) using the "Median Catch" (in '000t) vs. "Proportion < Bpa" summary performance statistics (top panel), and the "Average Catch Variation" statistic plotted against α (bottom panel) for three levels of r^2. The underlying functional form for the fecundity index vs. fecundity relationship is linear.

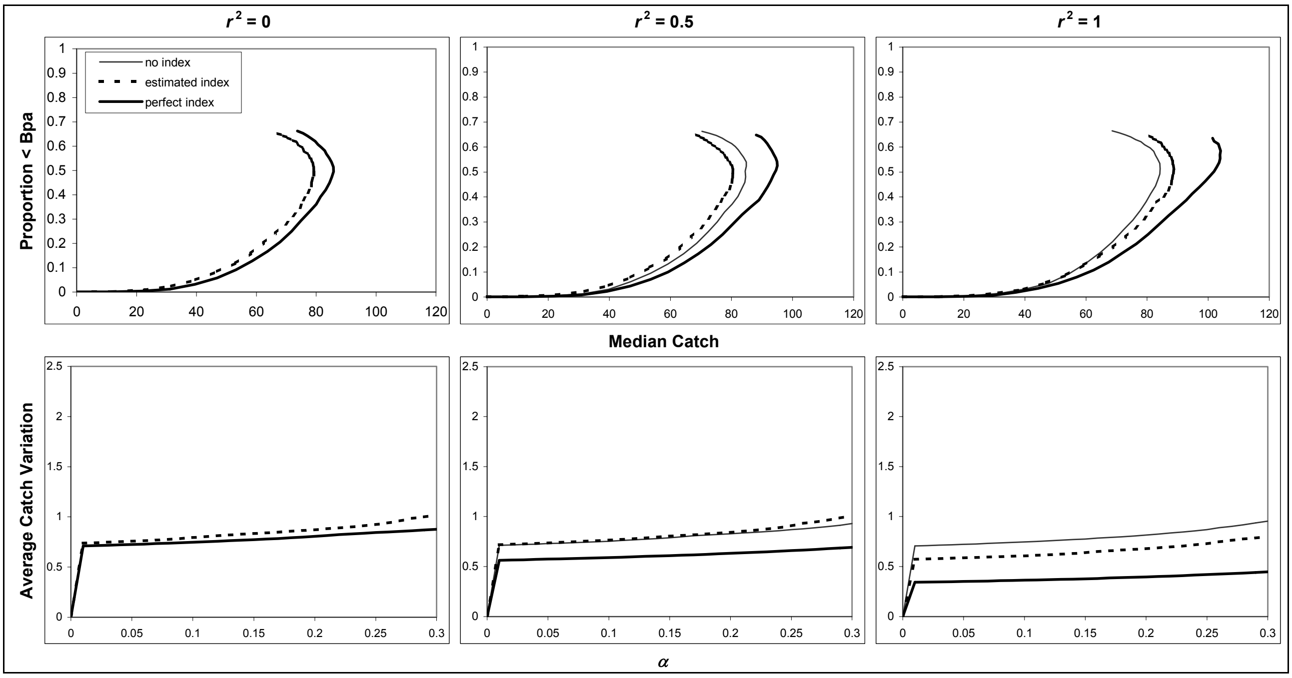


Figure 2 compares the three perceived SSB models for $r^2 = 0.5$, for a linear underlying functional form for the fecundity index - fecundity relationship, and for the case where both 10 and 30 years of data are used to estimated the parameters for the "estimated index" model. An improvement in terms of "Proportion < Bpa", "Median Catch" and "Average Catch Variation" is apparent when a longer time series of data are used for the "estimated index" model.

Figure 2 A repeat of the middle column of results in Figure 1 ($r^2 = 0.5$) using 10 (left column) or 30 (right column) years of data for the estimated index model (results for the other two perceived SSB models remain unchanged). The underlying functional form for the fecundity index vs. fecundity relationship is linear.

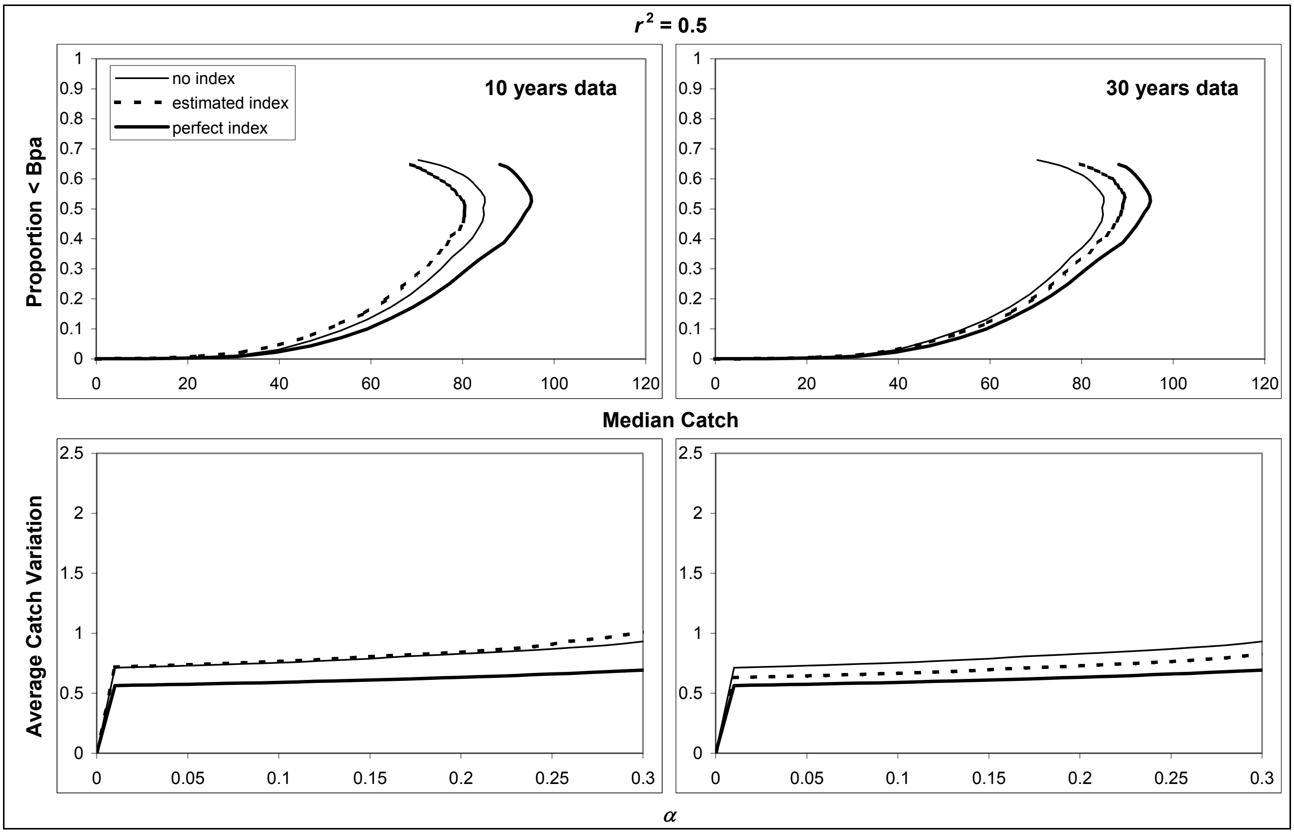


Figure 3 compares the three perceived SSB models for r^2 values of 0.5 and 1 and for three underlying functional forms for the fecundity index - fecundity relationship, assuming only 10 years of data available for the "estimated index" model. Comparing the performance of a given perceived SSB model for different r^2 values is tricky for the non-linear underlying functional forms (particularly the quadratic model) because the distribution of ε_y becomes less Normal-like (and more asymmetrical in the case of the quadratic underlying functional form) as r^2 is increased (equation 2). Therefore, performance of the "no index" model apparently improves with an increasing r^2 for the quadratic underlying form, even though it does not actually make use of an index, but this is artificial as it is purely due to the changing distribution of ε_y. The same effect (i.e. apparent improvement in the "estimated index" and "no index" models) is evident when moving from a linear to a quadratic underlying functional form. The overall effect of the distributional change in ε_y is that SSB^{perc} is more conservative for the quadratic underlying functional forms compared to the other functional forms, so that once again, the apparent improvement across functional forms is artificial. Therefore, in the case of Figure 3 (and 4) the performance for a given perceived SSB model should not be compared across r^2 values for the non-linear underlying functional forms, and should not be compared across underlying function forms. Comparisons between perceived SSB models for a given r^2 value underlying functional form are nevertheless still valid.

Figure 3 shows that the "no index" model outperforms the "estimated index" model for $r^2 = 0.5$, regardless of the underlying functional form for the fecundity index - fecundity relationship. When there is a very strong relationship between the fecundity index and fecundity ($r^2 = 1$), the reverse is true (the "estimated index" model outperforms the "no index" model) for a linear underlying function form, but not for the other two functional forms (logistic and quadratic). This is essentially because there is a mismatch between the underlying functional form (link 1) and the perceived functional form (link 3)

As shown in Figure 2, performance of the "estimated index" model improves throughout when it is based on 30 years of data (Figure 4) instead of 10 years of data (Figure 3). This improvement means that the "estimated index" model outperforms the "no index" model for both the linear and logistic underlying functional forms for r^2 values of 0.5 and above (Figure 4). In the case of the logistic underlying function form, this is probably possible because it is near-linear in a range of fecundity index values of highest probability (equations 2 and 5), and so is well estimated by a linear model (link 3) if the time series of data used in the estimation process is long enough. This is not the case, however, for the quadratic underlying functional form, for which a linear model is not a good approximation, even if a long time-series of data is available for estimating parameters.

Figure 3 A comparison of the three perceived SSB models assuming different underlying functional forms for the fecundity index vs. fecundity relationship (linear in the top, logistic in the middle and quadratic in the bottom panel), for r^2 values of 0.5 (left column) and 1 (right column). The vertical axis reflect "Proportion < Bpa", and the horizontal axis "Median Catch" (in '000t). The estimated index model uses 10 years of data.

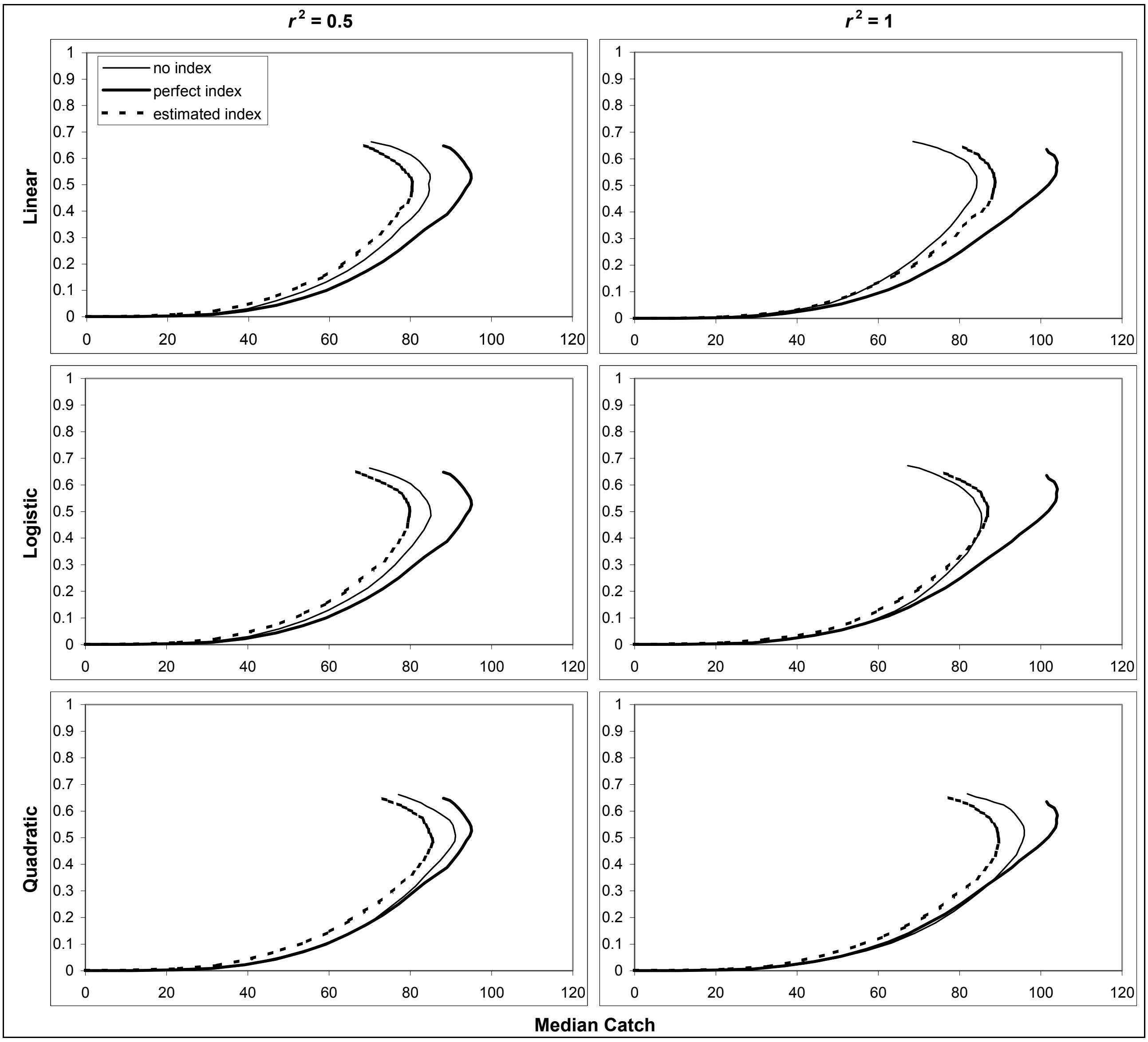
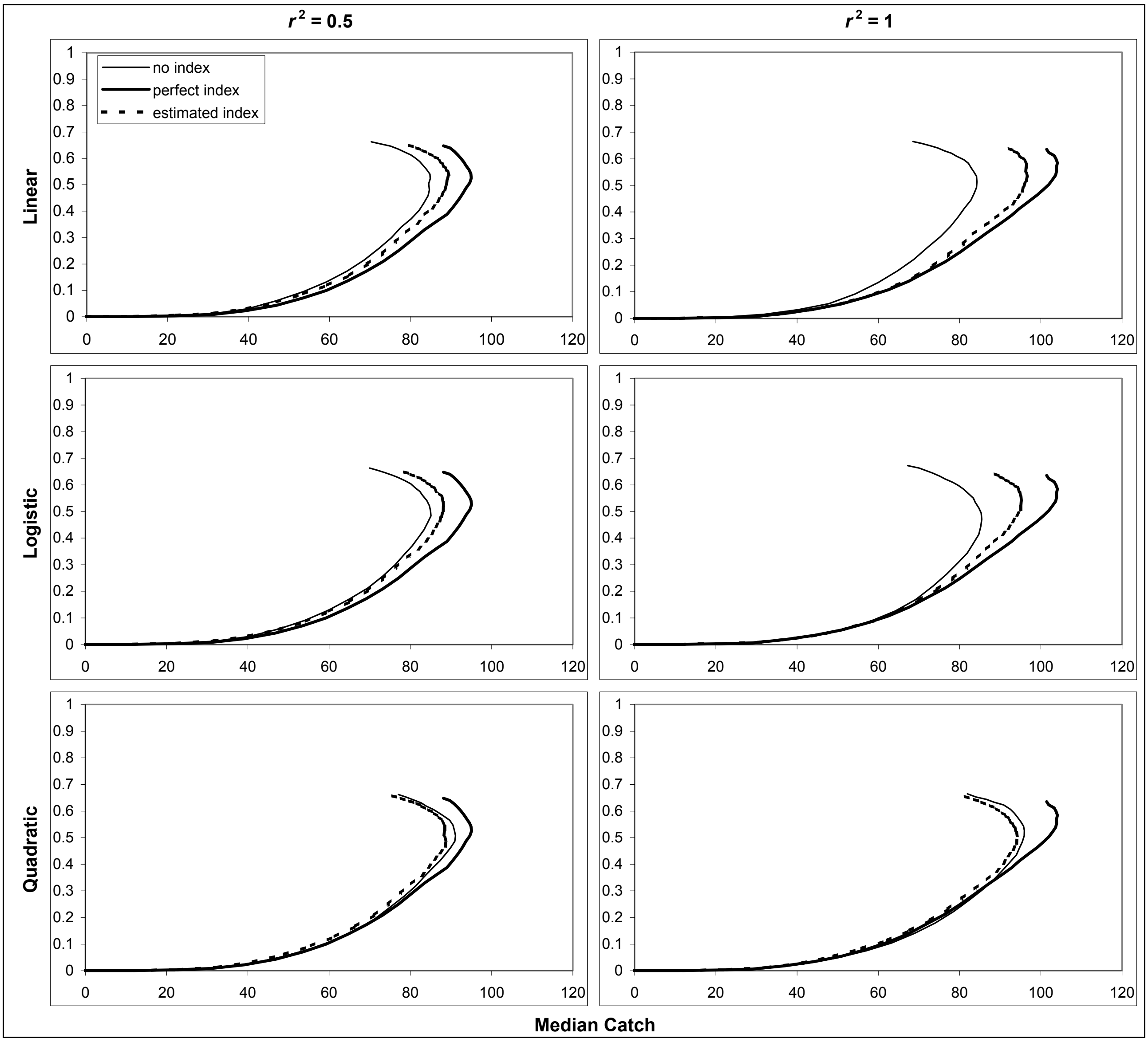


Figure 4 All details are as for Figure 4, except that the estimated index model uses 30 years of data. The results for the other two perceived SSB models therefore remain unchanged compared to Figure 3.



DISCUSSION

As with all simulation studies, the results of the study are completely reliant on the assumptions of the model. This study assumes that the index used as a proxy for fecundity is already verified, so that the length of the time series referred to throughout this study relates to only that portion of a time series of data used to develop the hypothesis about the index - fecundity relationship, and not the portion used to verify this hypothesis (Myers 1998). Typically, time series would need to be longer than 10 or 30 years (the values used in this study) to cope with both hypothesis development and verification. An analysis of different values for λ_{egg}, cv_{egg} and m warrants further investigation, as does the effect of assessment uncertainty (not currently accounted for) on results. Further this study only investigates the scenario of random variation in fecundity. Scenarios where a trend in fecundity was introduced, which would result in trends in the residuals from the assessment model fit were not simulation tested.

Given the values used for λ_{egg}, cv_{egg} and m in this study, that reflect the levels of process and observation error incorporated, the main conclusions of this study are that the use of a proxy for fecundity, to help obtain a perception of spawning stock biomass from egg abundance estimates, would improve management of western horse mackerel if:

- a strong relationship exists between the index used as a proxy for fecundity and fecundity itself,
- a relatively long time series of data is available to estimate the parameters of this relationship, and
- the underlying functional form of this relationship is well understood.

The "strength" of the relationship required for improved management if a fecundity proxy is used depends on the length of the time series available for estimating the parameters of the index - fecundity relationship. For example, results show that improvements are not possible for an r^2 of 0.5 if only 10 years of data are available for estimating these parameters. Very few studies show relationships as strong as $r^2 = 0.5$, and few have very long time series (Arctic cod being a notable exception, Marshall et al 2000). If the underlying functional form of the index - fecundity relationship is not well understood (i.e. the "perceived" form does not match the true underlying form), poorer performance is likely when using the proxy for fecundity compared to not using a proxy and assuming fecundity is constant, even if the relationship between the index and fecundity is very strong. Hence care must be taken when incorporating time series of proxies when the underlying relationships with fecundity are poorly described, weak or based on few data.

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APPENDIX

Spawning stock biomass:

The spawning stock biomass in the underlying model, referred to as the "true" spawning stock biomass, is calculated as follows.

$$SSB_y^{true} = \sum_{a=1}^{11+} N_{y,a} Q_a w_a^{stock} e^{-p_F\, s_a\, F_y \,-\, p_M\, M_a} \qquad y = 2002,...,2021 \qquad \text{A1}$$

where

$N_{y,a}$	is the number of fish aged a in year y;
Q_a	is the proportion of mature fish aged a;
w_a^{stock}	is the mean weight of fish aged a in the stock;
s_a	is the selectivity at age a;
F_y	is the fishing mortality in year y;
M_a	is the natural mortality at age a;
p_F	is the proportion of fishing mortality that occurs before spawning; and
p_M	is the proportion of natural mortality that occurs before spawning.

Recruitment:

Recruitment is generated using a combination of the Ricker stock-recruit function with parameters a and b estimated from a fit to stock-recruit estimates derived from the SAD model (ICES 2003b), and a process that allows the influx of very large recruitment with a frequency of roughly one in 20 years (equation 2). The recruitment variation and serial correlation parameters, σ_R and ρ_{ser} (equations 2 and 3), are derived from this fit.

$$N_{y,0} = \begin{cases} a\ SSB_y^{true}\ e^{-b\ SSB_y^{true}}\ e^{\sigma_R\, \zeta_y - \frac{1}{2}\sigma_R^2} & \text{for } \psi \geq 0.05 \\ 45 \text{ billion fish} & \text{for } \psi < 0.05 \end{cases} \qquad \text{A2}$$

where y = 2002,...,2021, ψ is independently drawn form a U[0; 1] distribution, and

$$\begin{aligned} \zeta_y &= \rho_{ser}\ \zeta_{y-1} + \sqrt{1-\rho_{ser}^2}\ \xi_y \\ \xi_y &\sim \mathrm{N}[0; 1] \end{aligned} \qquad \text{A3}$$

Numbers-at-age:

An age-structured deterministic underlying model is used, and is based on a separable assumption with regard to fishing mortality and selectivity, and assumes a plus group at age 11. The only stochastic part of the underlying model is recruitment (equations 2 and 3).

$$\left.\begin{array}{ll} N_{y+1,a+1} = N_{y,a}\ e^{-s_a F_y - M_a} & a = 0,...,9 \\ N_{y+1,11+} = N_{y,10}\ e^{-s_{10} F_y - M_{10}} + N_{y,11+}\ e^{-s_{11+} F_y - M_{11+}} & \end{array}\right\} \quad y = 2002,...,2021 \qquad \text{A4}$$

Calculating the fishing mortality and catch

The fishing mortality that results from applying TAC_y is calculated by solving for F_y from the following:

$$TAC_y = \sum_{a=0}^{11+} N_{y,a}\ w_a^{catch}\ \frac{s_a F_y}{s_a F_y + M_a} (1 - e^{-s_a F_y - M_a}) \qquad \text{A5}$$

An upper limit is placed on catching efficiency ($F_y \leq 20$, which results in

$\frac{s_a F_y}{s_a F_y + M_a} (1 - e^{-s_a F_y - M_a}) \leq 0.98$ for any age group, given the values used for s_a and M_a. The

resultant F_y is then used in equation 18 again to calculate the annual catch C_y (replace TAC_y with C_y in equation A5).