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Abstract: Complex fishery models are recommended to investigate the functioning of fisheries and assess the impact of management strategies, particularly spatial measures. However their use is limited due to the difficulty of parameterizing and gaining confidence in such parameter inflated models. Here we propose an approach that combines integration of information, fitting procedures and hypotheses testing to parameterize, validate and achieve the most plausible formulation of a model. The approach is applied to the anchovy fishery in the Bay of Biscay. Literature was first reviewed for parameter values determination. When contradictory or vague information was found, as was the case for reproduction duration, migration timing and egg mortality, two alternative modelling assumptions were proposed. Combining these assumptions led to eight alternative models. Each one was calibrated to assess missing parameter values for accessibility and adult mortality. Hindcast simulations were finally run to corroborate the alternative models with several time series of observations of different kind and at various aggregation levels. Summary statistics were calculated to quantitatively assess model skills and rank alternative parameterizations. The impacts of the intrinsic variability in selected parameters on the fishery dynamics were evaluated. The results suggested higher egg and adult mortality than formerly estimated and identified the most likely pattern of migration. The scoring system evidenced the strengths and weaknesses of each model. We conclude on the structural realism of the model making it relevant for management evaluation, but it is necessary to take into account the intrinsic variability in larval mortality as an important source of uncertainty in predictions.

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Dear Sir,

Please find enclosed the manuscript of an article we would like to submit for publication in Ecological Modelling. This paper deals with a methodology to parameterise a complex fishery model in a context of uncertainty to ultimately evaluate recovery and management plans. The proposed method uses simulations design to select the most relevant hypotheses of fishery functioning. The adequacy of several assumptions reviewed in the literature and sometimes contradictory is assessed. Model skill is characterized using summary statistics of model fit against multiple time series of observations. This approach is applied to the Bay of Biscay anchovy fishery.
We hope you find this paper suitable for publication in Ecological Modelling. My co-authors, Pierre Petitgas, Stéphanie Mahévas, Martin Huret, Youen Vermard and Andrés Uriarte fully participated in and accept responsibility for the work.

Yours sincerely,
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# Highlights

ISIS-Fish model parameters of the anchovy fishery in the Bay of Biscay are revised.

Alternative fishery parameterizations are considered under contrasted assumptions.

For each parameterisation unknown parameters are assessed by calibration procedures.

Summary statistics quantify the fit of hindcasted time series to multiple observations.

The most plausible parameterization is validated for management evaluation.

# Dealing with incomplete and contradictory information when parameterizing a complex fishery model? An example of the anchovy fishery of the Bay of Biscay.

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Abstract

Complex fishery models are recommended to investigate the functioning of fisheries and assess the impact of management strategies, particularly spatial measures. However their use is limited due to the difficulty of parameterizing and gaining confidence in such parameter inflated models. Here we propose an approach that combines integration of information, fitting procedures and hypotheses testing to parameterize, validate and achieve the most plausible formulation of a model. The approach is applied to the anchovy fishery in the Bay of Biscay. Literature was first reviewed for parameter values determination. When contradictory or vague information was found, as was the case for reproduction duration, migration timing and egg mortality, two alternative modelling assumptions were proposed. Combining these assumptions led to eight alternative models. Each one was calibrated to assess missing parameter values for accessibility and adult mortality. Hindcast simulations were finally run to corroborate the alternative models with several time series of observations of different kind and at various aggregation levels. Summary statistics were calculated to quantitatively assess model skills and rank alternative parameterizations. The impacts of the intrinsic variability in selected parameters on the fishery dynamics were evaluated. The results suggested higher egg and adult mortality than formerly estimated and identified the most likely pattern of migration. The scoring system evidenced the strengths and weaknesses of each model. We conclude on the structural realism of the model making it relevant for management evaluation, but it is necessary to take into account the intrinsic variability in larval mortality as an important source of uncertainty in predictions.

**Keywords**

Bay of Biscay Anchovy, Calibration, ISIS-Fish, Model skill assessment, Process modelling, Uncertainty

## 1. Introduction

Complex fishery models are needed to properly assess the impact of management rules, now involving spatial regulations and/or combinations of measures (Pelletier and Mahévas, 2005). We are defining complex models as dynamic, parameter rich models that explicitly account for processes related to resources and exploitation dynamics, in a spatial context. Because of their complexity, these models cannot be analytically solved and they rely on simulations (Mahévas and Pelletier, 2004). Although their use is recommended to account for spatial and seasonal processes and fleet behavior (Pelletier and Mahévas, 2005), the challenge of their implementation often discourages users. First, difficulties arise in the parameterization as numerous parameters must be estimated. In many existing fishery models, optimisation procedures are used to assess all parameter values simultaneously (Drouineau et al., 2010; Pech et al., 2001). This is not feasible with complex models given the high number of parameters, confounding effects and computation costs. Another approach consists of assessing parameters independently, using available knowledge and integrating this information in the model (Fulton et al., 2004; Kraus et al., 2009; Lehuta et al., 2010; Travers et al., 2006). Sensitivity analysis is recommended to identify the most influential parameters in the model and focus estimation efforts on these important ones (Saltelli et al., 2000). The review of available knowledge could lead to alternative and potentially contradictory views of how the fishery functions. In those cases, experts could help sort hypotheses or weight knowledge sources according to their reliability (Stefansson, 1998). If a valid likelihood function can be constructed, the Bayesian approach is well adapted to assign weights to alternative assumptions (see for instance Patterson, 1999). Otherwise alternative hypotheses should normally be stored for inclusion in uncertainty analyses (Hill et al., 2007). In any case, a rigorous validation of the final model must be carried out to support or conversely question the validity of the modelling choices. Validation often consists of visual comparisons between past time series and simulation outputs, with the constraint that these time series should not have been used for parameter estimation (Sterman, 1984). To provide more quantitative elements for model skill evaluation, several authors promote the use of specific metrics that reflect all aspects of model skill (Jolliff et al., 2009).

The parameterization of the simulation model ISIS-Fish (Pelletier et al., 2009) for the anchovy fishery in the Bay of Biscay illustrated all the steps of this modelling process. The anchovy (*Engraulis encrasicolus*) fishery in the Bay of Biscay has been closed from 2005-2010 after its biomass was assessed below biological limits (i.e. Blim: 21000t, ICES, 2009). Several restoration plans were considered to allow the reopening of the fishery. ISIS-Fish was used to model the fishery and to assess the impact of spatial management measures (Lehuta et al., 2010). The values of the fishing activity parameters were based on statistical analyses of logbook data whereas most of the biological parameters were obtained from a literature review (Lehuta et al., 2010). A sensitivity analysis was performed that pointed out that the most sensitive parameters were biological parameters related to mortality, reproduction and migrations (Lehuta et al., 2010). Accessibility was also revealed as sensitive in interaction with total fishing time, but the other parameters related to fishing activity were less influential.

In this paper we develop a comprehensive approach to model parameterization and use a case study of the Bay of Biscay anchovy fishery to explain how the best parameterization possible can be achieved given the knowledge at hand and the model structure. In light of the sensitivity analysis results, the choices made concerning the parameterization of sensitive processes were questioned. To refine parameterization of these sensitive processes, we used the model as an experimentation platform to investigate model fit to historical series by hindcast simulations. Parameters were classified into four categories. Three of the categories related to the level of uncertainty in parameter values: i) well-documented parameters or parameters for which a unique source of information was available, ii) parameters with contradictory values found in the literature and iii) parameters with poorly established values. Last set of parameters (iv) gather parameters that fluctuate from year to year (e.g., larval survival).

To deal with the two categories of uncertain parameters, we developed the following strategy. First, vague and contradictory information (ii) was summarised in two alternative possible parameter values. The combination of these alternative parameter values resulted in alternative model parameterizations. Secondly, hindcast simulations were run to calibrate inaccurately known parameter values (iii) and to assess the realism of the alternative parameterizations by quantitative comparison of simulation outputs and observations using various summary statistics.

Since the mechanisms responsible for the variability in category iv parameters were unknown, these parameters were considered as forcing variables. The impact of using the average value of fluctuating parameters rather than forcing them annually to observed values was assessed. Finally, we discuss the approach used and its relevance for model prediction.

## 2. Materials and Methods

### 2.1. Contradictory information

A distinction was made between accurately known biological processes or at least known through a unique source (category i) (Table 1) and processes that are either uncertain or contradictorily described in the literature (categories ii and iii) (Table 2). In the latter case, for the timing of migration to spawning grounds, the duration of spawning for small-sized anchovy and the value of egg mortality, the possible values were summarised in two alternative parameterizations. Uriarte et al. (1996) assumed that the migration of adults to spawning grounds occurs in winter but the exact timing is uncertain. The two contrasting hypotheses considered were a migration at the beginning of the winter season (January, hypothesis **MigJ**) or at the end (April, hypothesis **MigA**). Spawning is known to take place from April to August and fecundity, although sensitive, is relatively accurately known (Motos, 1996). However, individual spawning duration has not been characterized precisely. Pertierra et al. (1997) estimated spawning to last for three months, based on the number of batches and spawning frequency, while Motos (1996) gave a duration of 2.5 months and differentiated between fish of length smaller and larger than 14 cm. Five age-1 classes that potentially have different spawning durations are described in the model (Lehuta et al., 2010) according to their month of birth. Thus we defined a first hypothesis **R1** in which the two smallest age-1 classes (born in July and August of the previous year) spawn during two months only while the other age-1 classes (born earlier in the year) spawn during the full period of three months as adults do. In the alternative hypothesis **R2**, the three smallest age-1 classes (born from June to August) spawn for two months only, while the larger fish spawn during three months. Finally, a survey-based estimate of egg mortality in the Bay of Biscay (2000-2005) was 0.266 $day^{-1}$ (ICES, 2007) (**Megg1*)*** while Pertierra *et al*. (1997) assessed an egg mortality value of 0.56 $day^{-1}$ (**Megg2**) in the Catalan Sea. These two egg mortality rates were considered as possible starting points for mortality curves adjusted from birth to the end of the first reproduction (455 days) following a Pareto decay (Lo et al., 1995; Table 1). Combining the two alternative hypotheses for each of these three processes (egg mortality: ***Megg1 or Megg2***, spawning duration: ***R1 or R2*** and migration date to spawning grounds: ***MigA or MigJ***) resulted in eight (2x2x2) alternative parameterizations of the model.

## 2.2. Poorly known parameters

Adult mortality and accessibility were also sensitive parameters that were uncertain or poorly documented (categoty iii). Natural mortality can be considered almost constant after the first reproduction (Chen and  Watanabe, 1989), which applies to age 1 anchovies. This mortality for adults is estimated at 1.2 $year^{-1}$ by ICES (ICES, 2008). However, using a mortality decay Pareto model from the egg mortality **Megg1** (or **Megg2**) value to the adult mortality of 1.2 resulted in a very high survival rate from egg to recruitment (age 1), inconsistent with the estimated value of $10^{-5}$ (Petitgas and Massé, 2003). The value of adult mortality was thus considered questionable and the optimisation procedure described below (see 2.4) was applied to estimate the adult mortality at age 1.

No value was available in the literature for the accessibility parameter (sensu Seber, 1982), so we relied on expert judgement. According to experts, the accessibility of anchovy is mainly age-dependent. Three values of accessibility (q0, q1 and q2) were thus determined corresponding respectively to age-0 fish (until the first reproduction), age-1 and age-2+. The same fitting procedure based on the simplex algorithm was used as in Lehuta et al. (2010). It causes the estimated values to be dependent on the rest of the parameterization and they were re-estimated when any other parameter was changed.

## 2.3. Forcing variables

We distinguished between uncertain parameter values and parameters that may fluctuate from year to year due to unresolved causes (category iv). There was intrinsic variability in the anchovy spawning spatial distribution, time spent fishing and fishing strategies for the period 2000-2008. Larval survival also showed intrinsic variability, depending on environmental conditions. The individual-based larval drift and survival model (Huret et al., 2010) was used to estimate the potential survival of larvae depending on spawning area and date of birth. The effect of annual environmental conditions on larval survival was estimated by fitting an additive linear model to survival rates by year, month and area for the period 2000-2007 (Table 1). In hindcast simulations over the period 2000-2008, annual values of larval survival, observed stock distribution across spawning areas, and observed fishing effort and strategies of each fleet were used as forcing variables.

## 2.4. Hindcast simulations to fill knowledge gaps

For each of the eight parameterizations of the model, an optimisation procedure was used to assess the values of natural mortality of adults and the accessibility. As natural mortality and accessibility may have confounding effects, we used a sequential calibration on two contrasting periods. We first assessed natural mortality using a time series covering the period when no fishing occurred and then assessed accessibility during an open fishery period.

We first calibrated mortality curves over the period 2005-2008. Because of the anchovy fishing ban from 2005-2010, the population suffered only natural mortality in recent years, thus accessibility values were not required to simulate the period. A Pareto regression modelled the decline in mortality during larval and juvenile stages (Table 1). The Pareto model was fitted using a range of values for adult mortality. The best fitted outcome of the observed population growth rate, as estimated by the slope of the SSB time series over the period 2005-2008 (ICES, 2009), was retained for each of the eight alternative parameterizations.

Parameter values for accessibility coefficients q0, q1, q2 were optimised using the variable step simplex algorithm (Walters et al., 1991) by comparing the catches at age by quarter reported by ICES (2000-2004) to the simulated ones. The sum of squared differences (MSE) (least square minimisation) was used to measure how well the model fitted the data.

Other simulated outputs were then compared to observations that were not used for parameterization and calibration for the purpose of evaluating model skills and deciding on the most realistic alternative parameterization of the model among the eight considered. Available observations were: spawning stock biomass and recruitment biomass assessed by ICES (ICES, 2000-2008), average distribution of egg production per month over the spawning season (Allain et al., 2007a), monthly catches by fleet reported in logbooks for the period 2000-2004 and annual catches over the period 2000-2004 (ICES, 2008). Different summary statistics were used, which reflected particular aspects of the model fit:

- correlation of time series: $r = \left( \sum_{i=1}^{n} (O_i - \overline{O})(P_i - \overline{P}) \right) / \left( \sqrt{\sum_{i=1}^{n} (O_i - \overline{O})^2 \sum_{i=1}^{n} (P_i - \overline{P})^2} \right)$
- model prediction accuracy: $MSE = \frac{1}{n} \times \sum_{i=1}^{n} (P_i - O_i)^2$
- modelling efficiency (Stow et al., 2009):

$$MEF = \left( \sum_{i=1}^{n} (O_i - \overline{O})^2 - \sum_{i=1}^{n} (P_i - O_i)^2 \right) / \left( \sum_{i=1}^{n} (O_i - \overline{O})^2 \right)$$

where $P_i$ is the $i_{th}$ of n model predictions, $O_i$ the $i_{th}$ of n observations and $\overline{O}$ and $\overline{P}$ are the observation and prediction averages respectively. MEF measured how well the model predicts relative to the average of the observations.

Finally exploratory runs were performed to assess the impact of inter-annual variability in the parameters. The most plausible parameterization among the eight was run for the period 2000-2008 and inter-annual forcing factors (i.e. larval mortality, distribution across spawning areas, fishing time and strategies) were relaxed one by one as suggested by Mackinson et al. (2009*)*. The model forced with constant average values was also run. This helped us evaluate whether an average value in prediction was appropriate or whether scenarios needed to be considered. Results were explored using the same summary statistics.

For simulations, initial numbers of fish in each stage in January of the starting year were required. The ICES BBM model only provided the total biomass of recruits in January 2000 and the SSB in May 2000. The ICES ICA model (ICES, 2000) provided population numbers at age in May 2000. Recruit numbers at each stage were thus derived from recruit biomass converted into numbers at each stage using the survey-derived length-weight relationship and a theoretical length distribution. For adults, we used estimated biomass in

May and the demographic structure resulting from ICES ICA model and back calculated the number at age from May to January by correcting for mortality.

## 3. Results

### 3.1. Calibration

Adult mortality rates calibrated on population growth rate over the period 2005-2008 were much higher than the value of 1.2 used by ICES (from 1.63 to 3.03 depending on the parameterization) (Table 3). Accessibility values of juvenile fish (before the first reproduction) were 100 times lower than those of adults regardless of the model parameterization (Table 3). The largest differences between accessibility values (particularly for q1) occured for parameterizations in which egg mortality differed (Table 3). According to the least squares minimisation between simulated and observed catches, the best fit was obtained between simulated and observed catches for the parameterization with hypotheses **Megg2**, **R2** and **MigJ** (Table 3) and more generally for parameterizations assuming **Megg2**. Therefore egg mortality could be higher than previously thought or a high value could be necessary to compensate for other parameters.

### 3.2. Corroboration with observations

We used radar plots displaying summary statistic values on every output variables simultaneously to compare model performance according to the three fitting characteristics: correlation (r), accuracy (MSE) and efficiency (MEF) (Figure 1).

Temporal correlations ranged from 0.18 for the catches at age 2 to 0.99 for spawning distributions. Although the models were calibrated on catches at age, the temporal correlations seldom exceeded 0.8 for these output variables. Correlation values did not differ much between models, except for catches at age 2, for which hypotheses **Megg2** and **MigA** appeared more suitable (Figure 2).

MSE values differed considerably between output variables because of the variety of metrics and temporal scales. To be able to compare alternative parameterizations across output variables, the value displayed on the radar plot is the rank of each parameterization according to its MSE value (8 corresponding to the lowest MSE value: best, 1 to the highest: worst). The rank of the parameterization highly depended on the output variable considered. Annual catches, catches at age, biomass and spawning distribution appeared more accurately reproduced using models with hypotheses **Megg2** and **MigA**, while **Megg1** fitted better to catches of trawler fleets. The representation used enabled parameterizations to be ranked according to spawning distribution, which is probably the most direct consequence of the hypotheses on reproduction patterns. Although inter-annual variations were important particularly in July, the spatial and temporal distribution of egg production was close to the average pattern reported by Allain et al. (2007a) (Figure 3). Differences mostly concerned the month in which egg production peaks. The observed peak egg abundance in June could be achieved assuming **Megg2** and **R1** only. Therefore spawning duration for most of the age-1 fish could be as long as that of age-2 and spawning timing is probably influenced by age structure. Finally, model efficiency was relatively low with frequent negative values indicating that the observation average would be a better predictor than the model results. In particular, modelled catches of purse seiners profile 1 (CBol1), and trawlers profile 2 (CPel 2) were far from observations. Once again, the better model depended on the output variable considered. Parameterizations with **Megg2** gave poor results when considering catches of trawler fleets (particularly CPel2), mostly because catches in the first year are overestimated (Figure 4), but these parameterizations were appropriate for the majority of the other outputs.

Based on this ability to fit biomass and total annual catches, which represent a high level of process integration, the parameterization assuming **Megg2**, **R1** and **MigA** was selected.

3.3. Impact of inter-annual variations

Exploratory simulations were run with the selected parameterization (egg mortality hypothesis **Megg2**, first reproduction function (**R1**) and migration of adults in April (**MigA**)). We focused on the impacts of taking intrinsic variability into account on temporal correlations between simulated and observed variables. Each output variable reacted differently and revealed the process that most impacted its dynamics (Figure 5). Biomass, catches at age 0, recruitment and catches of purse seiners fleets, were highly influenced by the forcing by larvae survival. Relaxing the forcing generally improved the correlation except for catches at age 0, showing that the processes occurring between egg and recruit stages are not fully resolved. However visual validation (Figure 6) showed that forcing by the larval survival time series captured part of the biomass trend, although it anticipated the biomass drop that really occurred in 2002. Average migration had a low impact and generally decreased correlation while average effort significantly decreased the correlation for purse seiners profile 1. Consequently, scenarios are needed for larval survival and migration, as they largely influenced the dynamics. On the other hand, the average effort and strategies should be appropriate for most of the fleets except for purse seiner profile1 (CBol1).

## 4. Discussion

Our methodology enabled us to develop the most plausible parameterization of the Bay of Biscay anchovy fishery using a combination of 3 approaches: 1) literature review for well established parameter values, 2) hindcast simulations with alternative hypotheses when parameter values were conflicting, and 3) optimisation to estimate poorly known parameters. The selected parameterization provides a slightly different picture of the anchovy life cycle than previously envisaged: 1) egg and adult mortality may be higher than reported; 2) the spawning period may be as long for new recruits (one year old) as it is for adults, and 3) adults may return to the spawning grounds in April just before spawning. The egg mortality selected agreed with the values observed in the Mediterranean rather than in the Atlantic (ICES, 2007; Pertierra et al., 1997). Migration date however, was coherent with the catches of anchovy in winter in the north of the Bay of Biscay as reported in log-books. Simulation results gave insight into a likely functioning of the fishery that could be further tested by winter surveys for migration patterns or studies on physiology in relation to environmental conditions to improve knowledge of spawning duration mechanisms.

This approach proved that complex models can help investigate the coherence of our knowledge as well as provide plausible values for parameters that are difficult to measure such as natural mortality. They also reveal emergent properties of the system as a result of the interactions between explicit processes that are described independently.

Given model characteristics (high number of parameters, large simulation time), the use of literature values and the independent estimation of parameters (integration of information) was preferred to simultaneous optimisation of all model parameters. Also an integrated estimation (e.g. using likelihood) would require many data sources and their compliance with model assumptions, a situation seldom encountered (Pech et al., 2001). Integrating information in the model first required the inventory of knowledge and uncertainties. This step is also essential in operational management procedures applied toward the achievement of robust management (Hill *et al.*, 2007). It tends to be more largely carried out, at least qualitatively, through the use of pedigree matrix that aims to reflect the quality of data sources, knowledge and assumptions used in policy decisions (see for instance Ulrich et al., 2010). Sensitivity analysis (Lehuta et al., 2010) supported the identification of the most important processes to investigate. Here we went further in the approach by listing alternating hypotheses and ranking them based on quantitative criteria.

The method consisted of using available time series for calibration and validation of the model. It simultaneously enabled us to improve knowledge and falsify unlikely hypotheses (or combinations of hypotheses).

Fitting procedures were limited to few parameters. However the estimated values should be interpreted cautiously. The parameters are estimated conditional to assumptions made elsewhere in the model, and the estimated parameter values may thus compensate for the value of other parameters to achieve a good fit. The estimate of adult mortality can be discussed as an example. Firstly, the short duration of the calibration period (only four years) gives low robustness to the mortality estimate. Secondly, because the values appeared very sensitive to other assumptions of the model and the value of 3.03 was out of range according to experts, it should be interpreted in the context of our model. The biomass time series used for calibration resulted from an assessment model (ICES WGANSA, 2009) for which assumptions regarding recruitment (random) and adult mortality (1.2) differed from ours. Validation based on trends in scientific survey indices is perhaps an option to consider in future studies. For the same reasons, the calibrated values of the stock accessibility should also be interpreted carefully because compensating effects are likely to occur due to errors in the other parameters relating fishing effort with fishing mortality.

Our approach of corroboration against multiple time series could be seen as a concrete application of pattern oriented modelling (Wiegand et al., 2003). The use of several time series of observations guaranteed the model ‘structural realism'. In effect, the model cannot reproduce simultaneously multiple patterns observed at different scales and hierarchical levels if key processes are not captured realistically (Cury et al., 2008). Secondly, because of the multiple, confounding factors that can have synergistic or antagonistic effects on fishery dynamics, one needs more than a single series of observations to distinguish between several hypotheses of description for a phenomenon (Mackinson et al., 2009). It enables model developers to filter implausible combinations of hypotheses even if their effects are generally confounded. For instance, model fit on biomass was equivalent across parameterizations, as biomass is mainly driven by variation in recruitment. However, the underestimation of egg mortality in parameterizations with **Megg1** induced incompatible low proportions of age-2+ in the population and very low catches for these classes. Reducing spawning duration for one cohort and changing the date of migration had almost no effect on SSB, but it respectively modified the distribution of egg production in time and influenced the seasonality of catches.

Here we tried to make the validation step more objective by quantifying model skill through statistical criteria. This approach is largely applied for validation of coupled physical-biological models (Allen and  Somerfield, 2009; Jolliff et al., 2009; Stow et al., 2009) that often make use of geo-referenced validation data. Indeed parameterization of fishery models using fitting procedures generally requires all available data and, as a consequence, independent information is lacking for validation. It should be recognized that absolute validation of a model is merely impossible, and this notion could be replaced by a measure of model skill based on model predictions (Sterman, 1984). Though reference points could also be defined for correlation and model efficiency (Maréchal, 2004), defining a reference MSE value is rarely done. This could potentially be achieved by comparison of model MSE to observation error of the data as the model could not be expected to give more accurate predictions than the observations. However those observation errors are themselves rarely determined. Further developments of summary statistics for time series would also be necessary to complete the description. Moreover the best model is not always the one with the best fit (Mackinson et al., 2009), as illustrated here by the fit of biomass that appeared worst with the larval survival forcing, although the visual comparison proved that part of the pattern was captured.

Jolliff et al. (2009), proposed summary diagrams such as Taylor diagrams together with reference points to help summarise model skills, while Allen and  Somerfield (2009) relied on multivariate analyses. We ranked alternative parameterizations using radar plots for each criterion. This approach also allowed comparing visually the different parameterizations on different output variables. The selected parameterization was not unanimously supported neither across summary statistics, nor across output variables. Stefansson (1998) proposed to give preference to the most reliable knowledge sources, but again, reliability is hard to determine. When the sources are so conflicting that the model cannot explain all the data sources simultaneously, Pech et al. (2001) proposed an iterative procedure of partial fit and Stefansson (1998) suggested questioning model structure. Here we based our appreciation of reliability mostly on biomass and catches, as these output variables are relevant for predictions.

An advantage of the method was that it transparently evidenced the strengths and weaknesses of each parameterization and pointed out the errors we avoided by using the selected hypotheses. Even if reproducing time series gave confidence in the model, failures in fitting the model were also informative and offered the opportunity to reveal gaps in the current understanding of the system and provide indications of where further knowledge could be usefully gained. For example, Spanish purse seiner catches were underestimated in 2001 and French trawlers catches were overestimated over the first years (not shown). A possible explanation could be that Spanish purse seiners target bigger fish than the French trawlers, a hypothesis that could be verified by analysing fishery data further. The model is designed to enable the integration of knowledge when it becomes available. Finally some of these discrepancies between observed and modelled data can also be explained by the propagation of errors from the population sub-model to the exploitation sub-model. For instance, some of the output variables (catches at age 2-3) were better simulated without constrained larvae survival.

The ultimate aim of the model development is to evaluate the impact of a mixture of spatial and catch regulations that have never been enforced on this fishery. The present study has shown that the main processes were understood and successfully modelled and that past trends were reproduced when annual variability in some processes was forced. Consequently, we consider the model relevant and suggest that the rejected alternative hypotheses should not necessarily be included in a future uncertainty analysis. Yet, large natural variability in some parameters, mainly larval survival, limits prediction reliability and scenarios should be considered. Finally, the sensitivity analysis run on the preliminary version of the model (Lehuta et al., 2010) showed that even if uncertainties in some processes seemed to have low impact on population dynamics, interactions with management might result in changes in the relative importance of the sources of uncertainty. We thus recommend accounting for both the intrinsic variability and estimation uncertainty in prediction by running the model within an uncertainty analysis framework.

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Figure 1: Radarplots of the scores of each alternative parameterisation (coloured lines) against each output variable (radial lines) and summary statistics with best parameterisation at the outer ends (top left: correlation value, top right: rank (from 1 to 8) of the parameterisation according to its mean squared error value, bottom left: model efficiency). Biomass: time series of annual spawning stock biomass 2000-2008, Catch/y: time series of annual catches 2000-2004, Cage0 (resp. Cage1, Cage2, Cage3): time series of the catches at age 0 per quarter (resp. age 1, age 2, age 3+), CPel1 (resp. CPel2, CBol1, CBol2, CBolSp): time series of monthly catches by French pair trawler profile 1 2000-2004 (resp. French pair trawlers profile 2, French purse seiners profile 1, French purse seiners profile 2, Spanish purse seiners), R: time series of annual recruitment biomass, Sp. distr.: average distribution of egg production per month over the spawning season. See text for details on statistics.

Figure 2: Catches (numbers) of anchovy of age 2 per quarter over the period 2000-2004 as reported in ICES (2005) (black line) and as predicted by the alternative parameterisations (coloured lines). A: Megg1R1MigA; B: Megg1R1MigJ; C: Megg1R2MigA; D: Megg2R2MigJ; E: Megg2R1MigA; F: Megg1R2MigJ; G: Megg2R2MigA; H: Megg2R1MigJ.

Figure 3. Comparison of the average fraction of eggs produced each month (Allain et al., 2007a) (drawn lines) with box-whisker plots of the inter-annual variability in the estimates based on models assuming MigApr, Megg2 and R1 (A), MigApr, Megg2 and R2 (B).

Figure 4: Monthly catches (kg) of anchovy by the pair trawler fleet profil2 over the period 2000-2004 as reported in log-books (black line) and as predicted by the parameterisations with R1, MigApr and Megg1 (grey, continuous lines) R1, MigApr and Megg2 (grey, dashed lines).

Figure 5: Impact on model fit of the forcing variables. Simulations are run with all forcing variables (forced model), or with one forcing relaxed (average effort, average mortality, average migration) or with all forcing variables averaged (average model). Radarplot displays the correlation between observations and predictions (best at the outer end) for each simulation (coloured lines) and each output variable (radial lines).

Figure 6: Time series of population biomass in May (2000-2008) from ICES assessment of anchovy (Estimated SSB), and hind-casted with different scenarios: forced with larval mortality, spatial distribution and fishing effort (grey dots), leaving out the forcing factors one at a time (replaced by average values), and using no forcing at all (average).

Figure1
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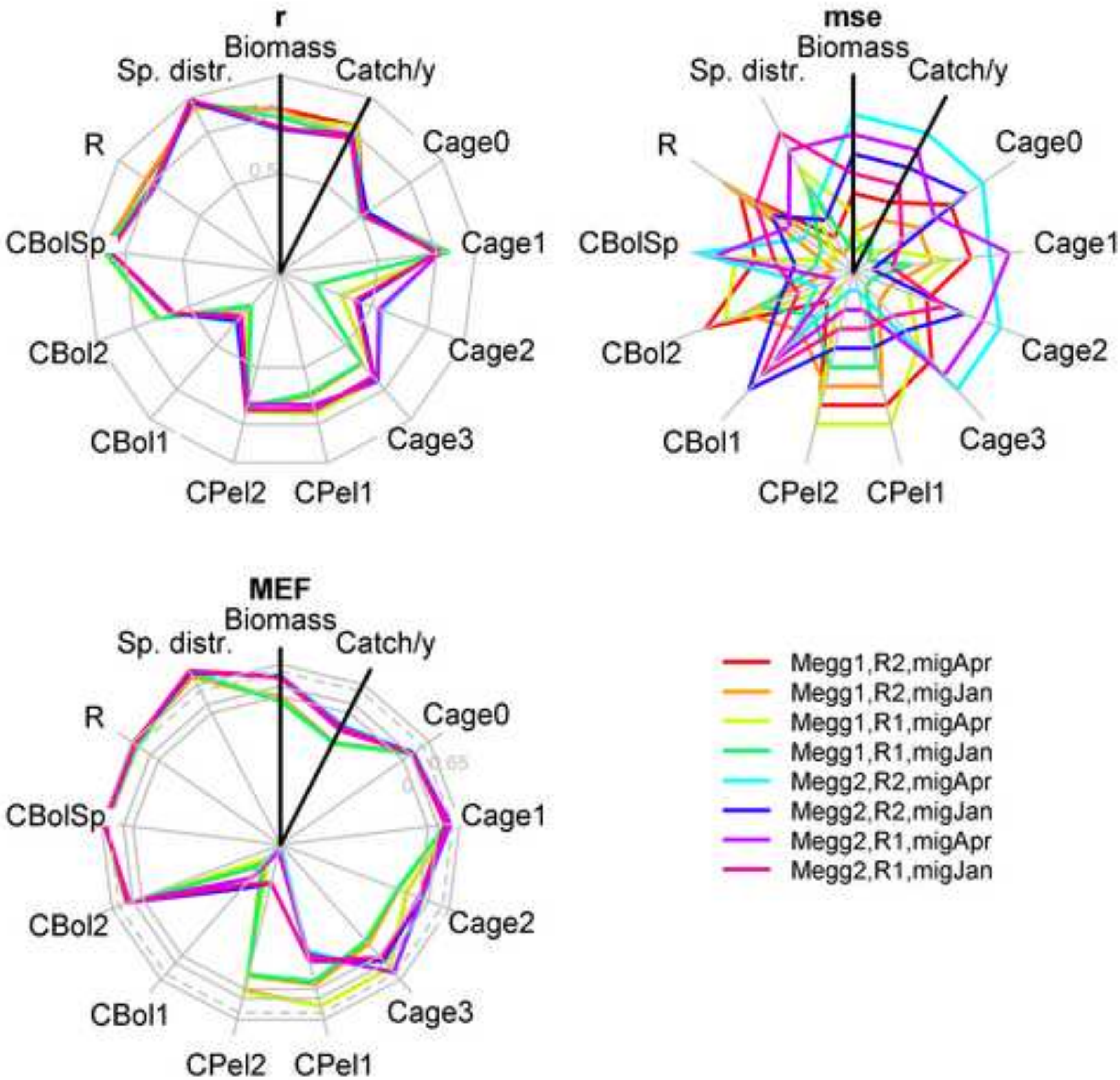

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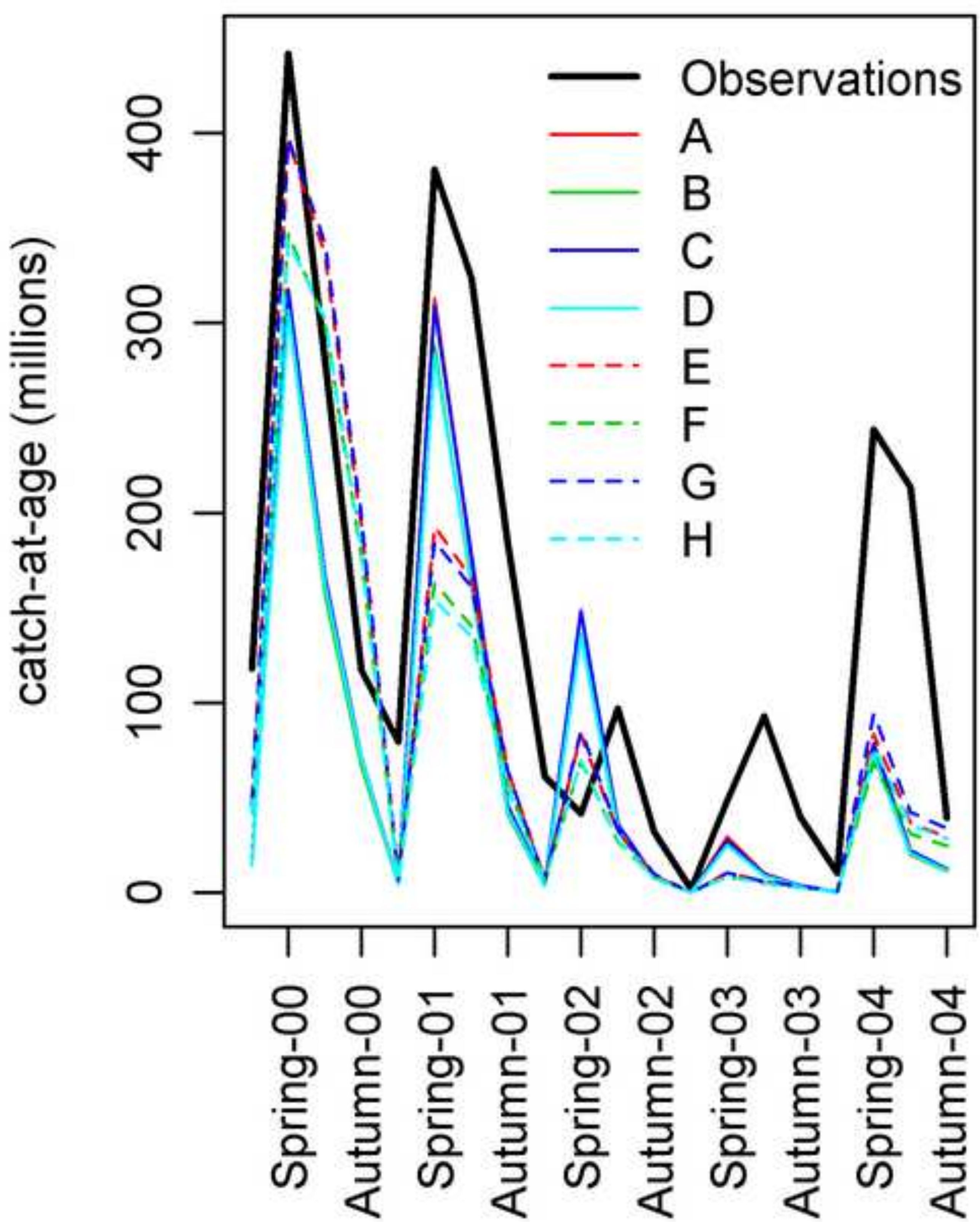

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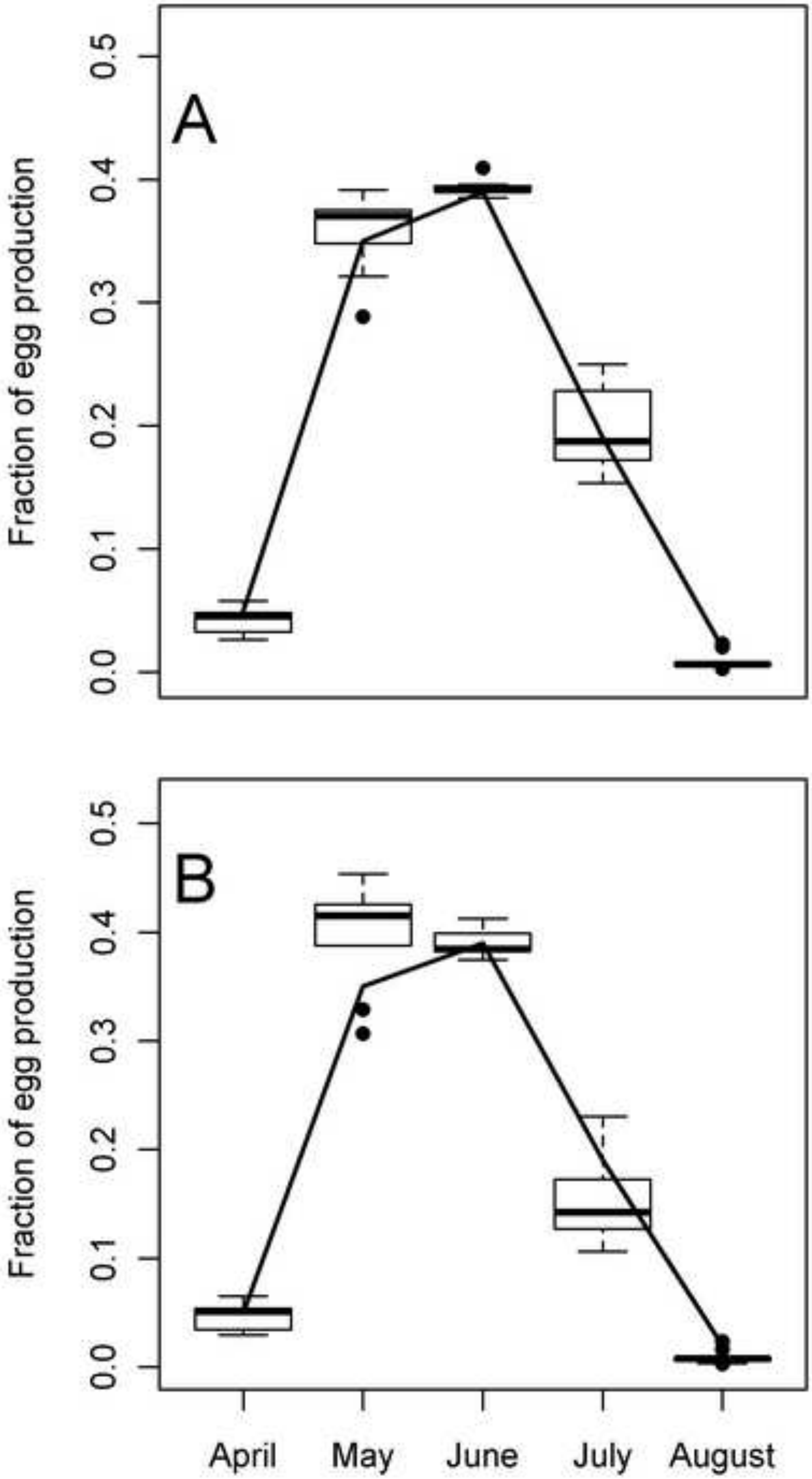

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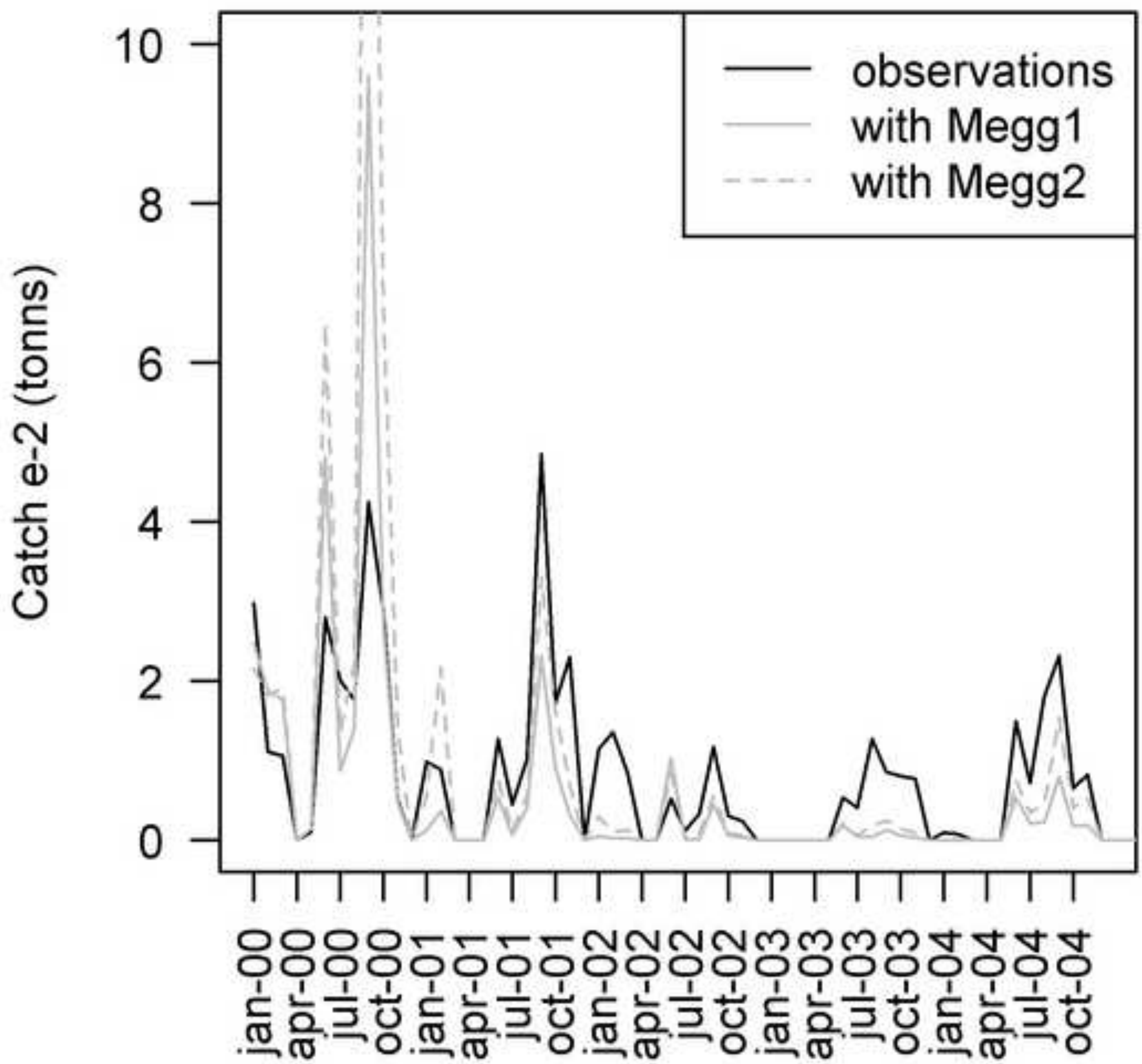

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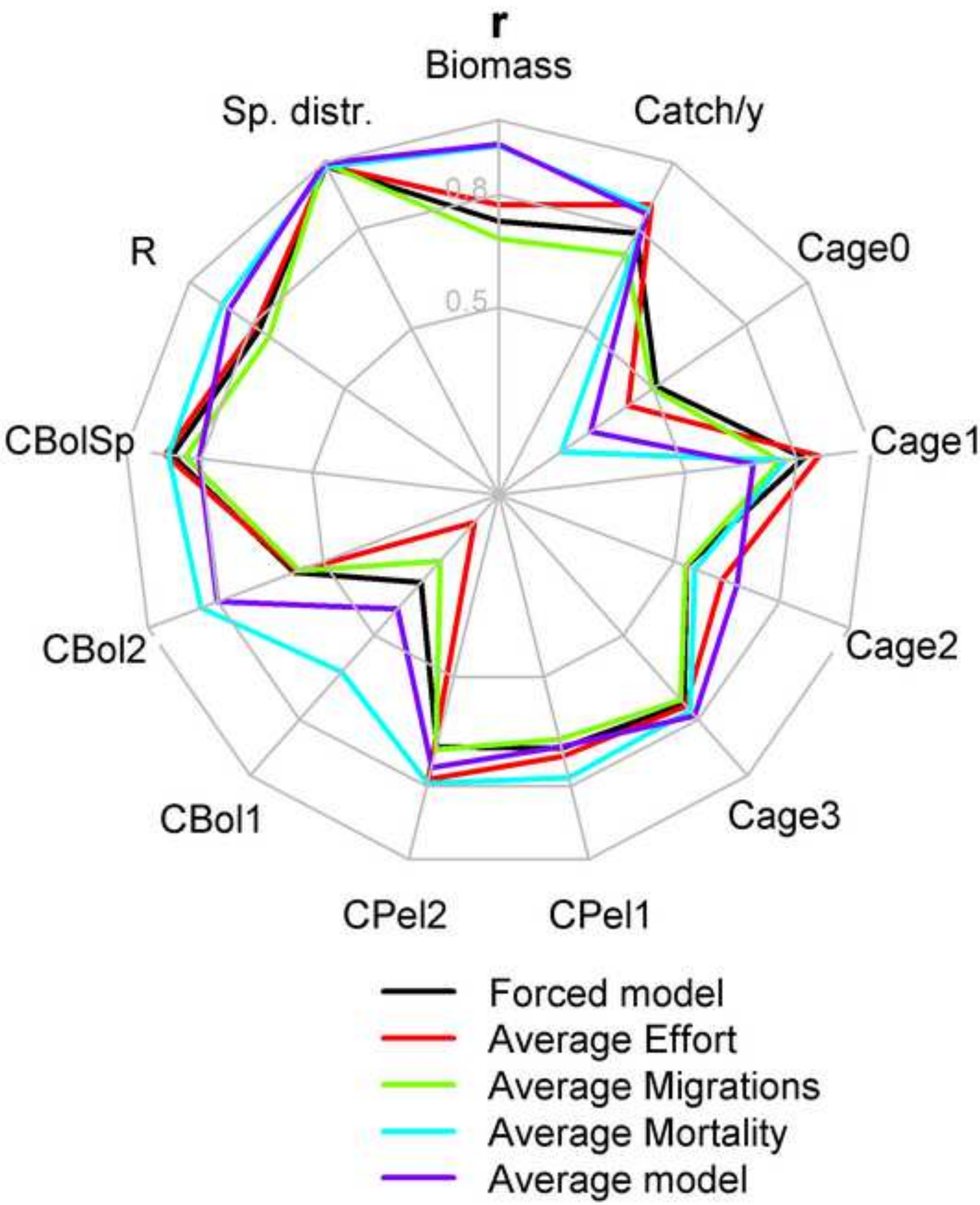

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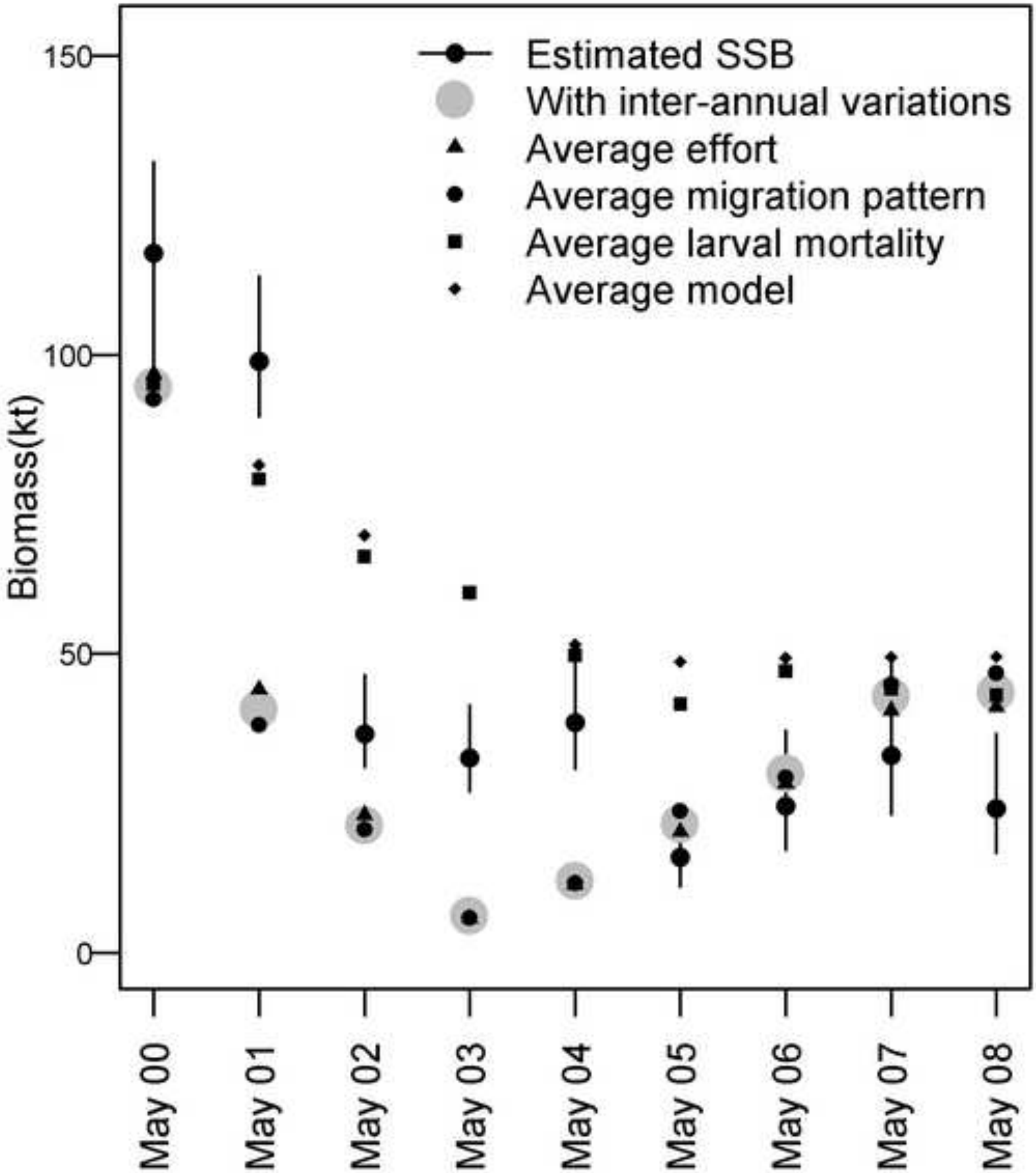

**Table1**

<table>
<tr><th>Process</th><th>Modelling assumptions</th><th>Parameter values</th><th>Reference</th></tr>
<tr><td colspan="4">Spatial organization</td></tr>
<tr><td>Population areas</td><td>Five population areas that correspond to habitats occupied seasonally by the different age groups</td><td></td><td>Vaz et al., 2002; Uriarte et al., 1996; Motos et al., 1996</td></tr>
<tr><td>Spatial distribution in spawning areas</td><td>Determined by migration coefficients</td><td>Percent of observed number-at-age in May per area each year. Average values (%) are reported below :
<table>
<tr><th>Area</th><th>Age-1</th><th>Age-2+</th></tr>
<tr><td>Gironde</td><td>47</td><td>29</td></tr>
<tr><td>Landes coastal</td><td>11</td><td>15</td></tr>
<tr><td>Landes Large</td><td>8</td><td>18</td></tr>
<tr><td>Rochebonne</td><td>27</td><td>33</td></tr>
<tr><td>North</td><td>7</td><td>5</td></tr>
</table></td><td>Motos et al., 1996 ; Pelgas surveys (2000-2008)<br>Vaz et al., 2002; Motos et al., 1996</td></tr>
<tr><td>Migration along Cantabrian coast</td><td>Supposed to occur only in years of great Anchovy abundance</td><td>Ignored</td><td>Uriarte et al., 1996</td></tr>
<tr><td>Feeding area</td><td>Area “North” defined based on fishing spatial distribution assuming that fishermen follow fish migration and cover the entire anchovy distribution area</td><td></td><td></td></tr>
<tr><td>Migration to feeding area in autumn</td><td>Adults migrate in August, recruits (1 year old) in September.</td><td></td><td>Uriarte et al., 1996; Catch analysis.</td></tr>
<tr><td>Population spatial distribution in autumn and winter</td><td>Determined by migration coefficients</td><td>65% of age-1+ biomass is in area “North” (Figure 1)</td><td>Evohe surveys</td></tr>
<tr><td>Larval drift and juvenile concentration</td><td>Definition of a coastal “Recruit” area where they migrate at the age of 3 months.</td><td></td><td>Allain et al., 2007b</td></tr>
</table>

| | | | |
|---|---|---|---|
| in coastal waters | | | |
| ***Vital rates*** | | | |
| Growth (cm) | Function of age (monthly scale) with update each month for juveniles, each year for adults. | Von Bertalanffy growth function<br>Linf = 18.77<br>K = 1.25<br>t0 = -0.17 | Pelgas, 2000-2005 |
| Weight (kg) | Function of length for adult in spring and summer and juveniles all year.<br>Function of age in autumn and winter. | 4.18 x length$^{3.2}10^{-6}$<br><br>age-1=0.018; age-2=0.031; age-3=0.04 | Pelgas, 2000-2005<br><br>Market sampling (ICES, WGMHSA, 2000-2004) |
| ***Mortality*** | | | |
| Juvenile mortality (month$^{-1}$) | Function of age, monthly updated for juveniles (until the end of the first reproduction) | Exponential decay (Pareto regression) between egg mortality and adult mortality. | Lo et al., 1995 |
| Weighting factor per area of the mortality of larvae | The value is derived from IBM results through linear modeling. | Gironde=0.9;<br>Landes coastal=1.33;<br>Landes offshore=0.96;<br>Rochebonne=0.97;<br>North=0.95 | Allain et al., 2007a; Hinrichsen et al., 2011 |
| Weighting factor per year of the mortality of larvae | The value is derived from IBM results through linear modeling. | | Hinrichsen et al., 2011 |
| ***Reproduction*** | | | |
| Fecundity | Function of month and dry weight (90% of fresh weight) | Apr.=200, May=500, Jun-Aug = 650 | Motos, 1996 |
| Spawning fraction | | Apr=0.18, May-Aug=0.25 | Motos, 1996 |
| Maturity | All individuals mature after their first winter | | Motos, 1996 |
| Sex ratio | | 0.5 | Motos, 1996 |
| Reproduction function | Linear. Biomass in the last years considered low and consequently | Number of eggs (t,area) = fecundity x spawning biomass(t, area) | |

| | | | |
|---|---|---|---|
| | far from saturation threshold. | | |
| Spawning timing and location | Depend on area and date. | Start mid-April in Gironde, Landes coast and Landes offshore; in May in Rochebonne; in June in North. | Uriarte et al., 1996 ; Allain et al., 2007a |

Table 1: Well-known population processes integrated in the model, with modelling assumptions, parameter values and references.

**Table2**

| Process | Modelling assumptions | Parameter values | Reference |
|---|---|---|---|
| Migration to spawning area | Juveniles (age-1): January<br>Adults (age-2+): either January (**MigJ**) or April (**MigA**) | | Uriarte et al., 1996, spatial distribution of fishing effort. |
| Egg mortality rate (day$^{-1}$) | | 0.266 (**Megg1**)<br><br>0.565 (**Megg2**) | Eggs survey, Somarakis et al., 2004; ICES 2006, 2007, 2008, 2009; Pertierra, 1997 |
| Adults mortality (year$^{-1}$) | U-shaped curve: age-2 mortality lower than age-1 and age-3 | 1.2 [0.5 ;3]<br><br>calibrated on 2005-2008 period | ICES WGMHSA, Chen and Watanabee, 1989 |
| Spawning duration | Depends on individual length at the beginning of the spawning season | 3 months for adults.<br>Oldest juveniles spawn for three months like adults, youngest for two months. Hypothesis **R1** states that youngest fishes are those born in July and August, while hypothesis **R2** states that youngest fishes are those born in June, July and August. | Pertierra et al., 1997; Motos, 1996 |
| Accessibility | Probability for a fish in a given area at a given season to be fished by a standard fishing unit with non-selective gear | calibrated on 2000-2004 period | |

Table 2: Poorly-known or contradictorily described population processes integrated in the model, with alternative modelling assumption or estimation method and references.

**Table3**

| | Parameterizations | | | Calibrated parameters | | | | RSS |
|---|---|---|---|---|---|---|---|---|
| | Egg mortality | Reproduction duration | Migration date | Adult mortality | q0 | q1 | q2 | |
| Hindcast models forced by past time series | **Megg1** = 0.266 | **R1** | April | 3.03 | 3.56e-5 | 4.68e-3 | 2.20e-3 | 2.66e18 |
| | | | January | | 3.23e-5 | 4.46e-3 | 2.41e-3 | 2.70e18 |
| | | **R2** | April | 2.97 | 3.59e-5 | 4.48e-3 | 2.18e-3 | 2.62e18 |
| | | | January | | 3.30e-5 | 4.29e-3 | 2.36e-3 | 2.66e18 |
| | **Megg2** = 0.565 | **R1** | April | 1.67 | 8.98e-5 | 2.66e-3 | 2.70e-3 | 2.36e18 |
| | | | January | | 8.35e-5 | 2.27e-3 | 3.31e-3 | 2.35e18 |
| | | **R2** | April | 1.63 | 8.44e-5 | 2.59e-3 | 2.70e-3 | 2.29e18 |
| | | | January | | 7.67e-5 | 2.18e-3 | 3.23e-3 | 2.28e18 |

Table 3: Calibration results of the adult natural mortality and accessibility coefficients (q0, q1 and q2) and corresponding residuals sum of squares value (RSS) between simulated and observed catches at age per quarter, for different scenarios of egg mortality, reproduction duration and migration date.