

# Modelling the dynamics of the deepwater shark *Centroscymnus coelolepis* off mainland Portugal

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**Abstract** – A statistical approach to evaluate the temporal trends in the abundance of female *Centroscymnus coelolepis* in Portuguese waters of ICES division IXa is presented. A state space model is used, which integrates all the available information of the species' life history as well as knowledge of its biological dynamics. The model involves two processes that run in parallel: a non-observed process (the state process) that describes the annual female population abundance and an observational process of annual fisheries catches in numbers, assumed to be measured with error. Estimation is done within the Bayesian paradigm using sequential importance sampling with resampling. To evaluate the sensitivity of the model to the prior distributions chosen for the parameters, three scenarios with different levels of prior information were considered. Trends in population abundance level and the abundance levels themselves are quite similar in the two scenarios using biological information, but the model that incorporated all the available biological information in the priors provided the best fit to the observed data. The results indicate that taking into account the main biological drivers and the fishing information in the same state space model provides a coherent picture of the population abundance trends, further suggesting that the fishing impact on the population inhabiting Portuguese mainland waters was low.

**Keywords:** Abundance temporal trend / State-space model / Bayesian analysis / Portuguese dogfish / NE Atlantic Ocean

## 1 Introduction

The low productivity and long generation times that characterize elasmobranchs in general make this group particularly susceptible to fishing (Hoenig and Gruber 1990). This susceptibility is heightened for deepwater species since population recovery rates are known to decrease with the increasing depth (Simpfendorfer and Kyne 2009).

In the Northeast Atlantic, deep-water elasmobranchs have been caught by European fleets in trawl, longline and gillnet fisheries. The first two fisheries have been extensively described (ICES 1998, 2004; Machado and Figueiredo 2009). Before the European Union (EU) regulation (EC 1359/2008) that prohibited the landing of deep-water sharks, the Portuguese dogfish, *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864, and the leafscale gulper shark, *Centrophorus squamosus* (Bonnatere, 1788), were the main landed bycatch species in these fisheries (Figueiredo et al. 2005; ICES 2004; Johnston et al. 2005). These two species were also the targets of the gillnet fishery that was initiated in the mid-1990s on the continental slopes west of the British Isles, north of Shetland and at Rockall and Hatton

Banks (Hareide et al. 2005). Insufficient detail in the information available for this fishery precluded a robust analysis of the fishing activity (Large et al. 2009).

Historically, elasmobranchs have generally been of low economic value and catches have been poorly documented (Camhi et al. 1998). In EU fisheries, it has been a common practice to record landings of all deep-water shark species collectively under generalized categories such as “various sharks not elsewhere identified”, “siki sharks”, and “dogfish sharks not elsewhere identified”. As a result, the International Council for the Exploration of the Sea (ICES), the body responsible for providing advice on stocks exploited in EU waters, has evaluated historical trends in abundance of *C. coelolepis* and *C. squamosus* using a combined index of abundance (ICES 2004, 2007). However, this procedure is considered inappropriate due to the different life histories of the two deep-water shark species, which probably have different sensitivity to fishing. This was emphasized at the 2010 ICES Benchmark Workshop on Deep-water Species (WKDEEP), during which a draft of the present approach to evaluate the status of deep-water shark stocks was presented (ICES 2010). However, its application is dependent upon an acceptable reconstruction of the catch and effort data by species, for all the fleets that operated in the NE Atlantic, which was impracticable. As a result, further

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information, particularly greater resolution in the data, was required to clarify the proportion estimates, since without detailed fishery data it would not be possible to get robust time series of catch by species (ICES 2011).

*C. coelolepis* is a deep-water shark with a worldwide distribution, occurring in the western regions of the Indian and Pacific Oceans and in the Atlantic Ocean, where it is frequent from Iceland to Senegal and in Namibia and South Africa (Compagno et al. 2005). The stock structure of *C. coelolepis* in the NE Atlantic is still unknown but, for assessment purposes, ICES considers the existence of a single stock of *C. coelolepis* in NE Atlantic (ICES 2007).

Genetic studies involving specimens caught in the NE Atlantic area were inconclusive in identifying possible local populations (Verissimo et al. 2011). However, the hypothesis that they exist is not excluded (ICES 2010) and is supported by the occurrence of females in all maturity stages in the different fishing grounds (Clarke et al. 2001; Figueiredo et al. 2008; Girard and Du Buit 1999), so that the species may be able to complete its entire life cycle within a specific area.

In Portuguese waters ICES Division IXa, deep-water sharks are mainly caught as a bycatch species in the long-line fishery that targets black scabbardfish, *Aphanopus carbo* Lowe, 1839 (Machado and Figueiredo 2009). Unlike other EU fleets, Portuguese landings data on deep-water shark species have been recorded by species. These data, together with the corresponding fishing effort data, enables a complete study of *C. coelolepis* in Portuguese waters, which cannot be performed for the whole NE Atlantic area with the currently available data.

The present paper explores the adequacy of an analytical assessment approach developed to evaluate the status of this southern component, which integrates both fishing data and the available knowledge of the biology (growth, fecundity and embryonic development) and the dynamics of the species. To simplify the model, only females are considered since there is no evidence of exploitation targeting males that would imply a change on the 1:1 sex ratio structure. Additionally, females are key to the population dynamics because, under the model setting which represents the actual dynamics, the production of offspring is highly dependent upon the number of females in the population. The approach involves a state space model that divides the female population system dynamics into two processes: the unobserved process that describes the female population abundance in number, and the observational process that deals with the annual catches, also in number. Estimates of female population abundance in number across the time range and the posterior estimates of the species vital parameters and fishing mortality are the main outputs.

## 2 Materials and methods

### 2.1 Fishery data

Annual total landings of *C. coelolepis* from the deep-water fleet operating in Portuguese waters are available for the period between 1989 and 2008. Before 2007, species misidentification and discarding of deep-water sharks could be considered negligible because the available quota in Portuguese waters was sufficient to land all the bycatch in the black scabbardfish

fishery. After 2007, due to the restrictive quota, misreporting may have happened. Therefore, only landings for the period from 1989 to 2006 are considered in this paper. Over the study period, *C. coelolepis* landings were between 454 and 927 tons per year with a gradual decrease over time.

The annual catches in number,  $Y_t$ , were determined following the approach described by Quinn et al. (1983) as  $Y_t = C_t/\bar{W}$ , where  $C_t$  is the total catch in weight in the year  $t$  and  $\bar{W}$  is the individual mean weight estimate. Data on  $C_t$  is available from the Portuguese national fishery authorities (DGRM) database. The estimate of  $\bar{W}$  was obtained from the landing sampling program under the European Union Data Collection Regulation (Council Regulation (EC) No 1543/2000) that takes place in the landing port of Sesimbra (the most important landing port for deep-water species in Portugal mainland). The annual female catches, in number, were determined using  $Y_t$  and the sex ratio estimates at landings. It is noticed that no apparent trend was detected in the mean weight over the years and, for sex, as the differentiation is macroscopically detected, the 1:1 value adopted corresponds to the expert judgment from observation at the landing port.

In order to estimate the standardized fishing effort by year,  $E_t$ , where the effort unit adopted is fishing day, two steps were taken. First, a generalized linear model (McCullough and Nelder 1989) using lognormal residuals and an identity link function was adjusted to the landed weight of the species by fishing day (CPUE). These data were also available from the DGRM database for the time period of 1989–2006. The final model included the following explanatory variables: the vessel technical characteristics, gross registered tonnage, length-over-all and engine horse-power, as well as year, trimester, total landed weight of all species and percentage, in weight, of black scabbardfish. These variables were selected, using the AIC criterion, from a larger set that also included month and vessel identification. Residual graphical analysis was used to evaluate the adequacy of model assumptions. Finally, the  $E_t$  estimates were calculated through the relationship  $E_t = C_t/CPUE_t$ , where the standardized  $CPUE_t$  corresponds to the predicted CPUE for a standard vessel in year  $t$  (Maunder and Punt 2004).

### 2.2 Model

The model describes the simultaneous temporal evolution of a non-observable population state process that corresponds to the species abundance and an observational process of annual catches. Under the model, the population of females is represented by a state vector of five components. The components include specimens grouped according to criteria associated with maturity and vulnerability to fishing. The first component, denoted by  $n_{b,t}$ , is the number of non-recruited juveniles with total length (TL) smaller than 70 cm ( $TL < 70$  cm), that in year  $t$  have not yet been recruited to the fishery. Females of these sizes are almost never caught. The next two components represent the abundance of females that have survived fishing in year  $t$ : the juveniles ( $70$  cm  $< TL < 101$  cm) and the adults ( $TL > 101$  cm), i.e., with length larger than the length-at-first maturity (Figueiredo et al. 2008), denoted respectively by  $n_{j,t}(\bar{F})$  and  $n_{a,t}(\bar{F})$ . The final two components

represent the number of juvenile and adult females fished in year  $t$  and are denoted by  $n_{j,t}(F)$  and  $n_{a,t}(F)$ , respectively.

The state vector,  $\mathbf{n}_t$ , associated with the described population structure at year  $t$  is represented as  $\mathbf{n}'_t = (n_{b,t} \ n_{j,t}(\bar{F}) \ n_{a,t}(\bar{F}) \ n_{j,t}(F) \ n_{a,t}(F))$ . The population state process is stochastically derived from a deterministic general process whose annual evolution can be described by the relation  $\mathbf{n}_t = P^* \mathbf{n}_{t-1}$ , where  $P^*$  is a Lefkovich projection matrix (Caswell 2001).

For the stochastic model, it is assumed that females act identically and independently (IID hypothesis), and the annual evolution is formulated in terms of the conditional expected values of the state process which is assumed to be a first order Markov process:  $E[\mathbf{n}_t | \mathbf{n}_{t-1}] = P \mathbf{n}_{t-1}$ , where  $P$  describes the long term average effect of the stochastic process. The density dependency is not considered in the model because the information available does not provide ways to quantify its effect. Furthermore Last and Stevens (2009) suggest that some shark species are less prone to inter-annual environmental effects than teleost stocks.

To model the complexity of the population dynamics, the overall state process is decomposed into several subprocesses linked with the species life cycle which are judged vital for the dynamics of the species: *survival to natural mortality*, *class transition*, *birth* and *survival to fishing*. These subprocesses are considered to happen consecutively in time, always in the same order, with each subprocess only depending on the one that has occurred immediately before. Fishing is the last subprocess, i.e., in each year, females are assumed to be fished after all the other subprocesses have taken place.

For the deterministic version, the decomposition into subprocesses is converted into the following for the projection matrix  $\mathbf{n}_t = F^* B^* C^* S^* \mathbf{n}_{t-1}$ , where the corresponding matrices  $F$ ,  $B$ ,  $C$  and  $S$  for the stochastic formulation represent the long term average effect of the subprocesses survival from fishing, birth, class transition and survival from natural mortality, respectively. Similarly,  $E[\mathbf{n}_t | \mathbf{n}_{t-1}] = FBCS \mathbf{n}_{t-1}$ .

Under the Markovian assumption, the process is completely defined if the state process distribution is known at a certain time  $t$  conditionally on the process at the previous time point:  $\mathbf{n}_t \stackrel{d}{=} H_t[\mathbf{n}_{t-1}]$ , which can be further decomposed according to the various subprocess distributions as:

$$\begin{aligned} \mathbf{u}_t^S &\stackrel{d}{=} \mathbf{H}_t^S[\mathbf{n}_{t-1}] & \mathbf{u}_t^C &\stackrel{d}{=} \mathbf{H}_t^C[\mathbf{u}_t^S] \\ \mathbf{u}_t^B &\stackrel{d}{=} \mathbf{H}_t^B[\mathbf{u}_t^C] & \mathbf{n}_t &\stackrel{d}{=} \mathbf{H}_t^F[\mathbf{u}_t^B], \end{aligned}$$

where, for each time  $t = 1, \dots, T - 1$ ,  $\mathbf{u}_t^S$ ,  $\mathbf{u}_t^C$ ,  $\mathbf{u}_t^B$  and  $\mathbf{u}_t^F$  represents the state vector after each of the subprocesses mentioned before.

Due to the IID hypothesis, binomial models are assumed for the distributions of all the subprocesses changing components. For the first subprocess, the probability of surviving natural mortality, represented by  $\phi_S$  is assumed to be equal for the three components. Therefore,

$$\mathbf{u}_t^S \sim \mathbf{H}_t^S(\mathbf{n}_{t-1}) : \begin{pmatrix} u_{b,t}^S \sim \text{Bi}(n_{b,t-1}, \phi_S) \\ u_{j,t}^S \sim \text{Bi}(n_{j,t-1}(\bar{F}), \phi_S) \\ u_{a,t}^S \sim \text{Bi}(n_{a,t-1}(\bar{F}), \phi_S) \end{pmatrix}. \quad (1)$$

For the subprocess of class transition,  $C_b$  represents the probability that a non recruited juvenile transits to the juvenile stage and, similarly,  $C_j$  represents the probability that a juvenile transits to the adult stage. After the class transition subprocess takes place, the population vector is represented as

$$\begin{aligned} \mathbf{u}_t^C &\sim \mathbf{H}_t^C(\mathbf{u}_t^S) : \\ &\begin{pmatrix} u_{b,t}^C \sim \text{Bi}(u_{b,t}^S, 1 - C_b) \\ u_{j,t}^C = Y[u_{j,t}^S] + (u_{b,t}^S - u_{b,t}^C), \text{ with } Y[u_{j,t}^S] \sim \text{Bi}(u_{j,t}^S, 1 - C_j) \\ u_{a,t}^C = u_{a,t}^S + (u_{j,t}^S - Y[u_{j,t}^S]) \end{pmatrix}. \end{aligned} \quad (2)$$

In the birth subprocess, the binomial distribution for the number of newly born female offspring that survive has parameters  $(f u_{a,t}^C, p_B)$ , where  $f$  is the maximum number of embryos from one litter,  $u_{a,t}^C$  is the number of adult females at year  $t$  and  $p_B$  is the probability that an embryo produces a surviving female during a one-year period. The population vector after the birth subprocess can be represented as:

$$\begin{aligned} \mathbf{u}_t^B &\sim \mathbf{H}_t^B(\mathbf{u}_t^C) : \\ &\begin{pmatrix} u_{b,t}^B = u_{b,t}^C + X[u_{a,t}^C], \text{ with } X[u_{a,t}^C] \sim \text{Bi}(f u_{a,t}^C, p_B) \\ u_{j,t}^B = u_{j,t}^C \\ u_{a,t}^B = u_{a,t}^C \end{pmatrix}. \end{aligned} \quad (3)$$

For the fishing subprocess, the distributions of the number of survivors from fishing of either juveniles or adults are assumed to be binomial. In the expression below for the population vector after this subprocess takes place,  $\phi_{jt}$  and  $\phi_{at}$  represent the respective probabilities of a juvenile and an adult being fished in year  $t$ ,

$$\mathbf{n}_t = \mathbf{u}_t^F \sim \mathbf{H}_t^F(\mathbf{u}_t^B) : \begin{pmatrix} n_{b,t} = u_{b,t}^B \\ n_{j,t}(\bar{F}) \sim \text{Bi}(u_{j,t}^B, 1 - \phi_{jt}) \\ n_{a,t}(\bar{F}) \sim \text{Bi}(u_{a,t}^B, 1 - \phi_{at}) \\ n_{j,t}(F) = u_{j,t}^B - n_{j,t}(\bar{F}) \\ n_{a,t}(F) = u_{a,t}^B - n_{a,t}(\bar{F}) \end{pmatrix}. \quad (4)$$

The observational process is a stochastic function of the unknown states and its complete realization can be represented as  $\{y_t, t = 0, 1, \dots, T\}$ , where  $y_t$  corresponds to the total number of fished specimens at year  $t$ , which are assumed to be observed with error. For the present purposes, a symmetric error model with constant coefficient of variation was adopted for the estimates of catches. A normal distribution with the conditional mean  $E[y_t | \mathbf{n}_t] = n_{j,t}(F) + n_{a,t}(F)$  and standard deviation proportional to the mean is admitted:

$$y_t | \mathbf{n}_t \sim N(n_{j,t}(F) + n_{a,t}(F), \psi^2(n_{j,t}(F) + n_{a,t}(F))). \quad (5)$$

A non-informative gamma distribution was chosen for the  $\psi$  prior distribution, which is a common choice for these dispersion parameters, see Lunn et al. (2012) for example.

Finally, the state space model representing the simultaneous evolution of the state and observational processes is described by the following set of probability density functions:

$$g_0(\mathbf{n}_0; \Theta), \quad g_t(\mathbf{n}_t | \mathbf{n}_{t-1}; \Theta); \quad f_t(y_t | \mathbf{n}_t; \Theta),$$

**Table 1.** Description of the subprocesses parameters.

Parameter	Subprocess	Prior dist.	Description
$\phi_S$	Surviving	Beta	Probability of surviving natural mortality. Expected value is $E[\phi_S] = e^{-M}$ , assuming an exponential model for the individual lifetime. The annual natural mortality rate, $M$ , is set equal for all the population stages and estimated by $M = -\ln(p)/Age_{Max}$ (Hewitt and Hoenig 2005), where $Age_{Max}$ is the maximum age attained by the species and $p$ is the proportion of the unfished population that reaches that age. $Age_{Max} = 70$ years, equal to the estimate for <i>C. squamosus</i> (Clarke et al. 2002), and $p = 0.01$ (value commonly adopted for long-lived species).
$C_b$	Class transition	Beta	Probability that a non recruited juvenile transits to the juvenile stage (see Appendix A1).
$C_j$	Class transition	Beta	Probability that a juvenile transits to the adult stage (see Appendix A2).
$p_B$	Birth	Beta	Probability that an embryo produces a surviving juvenile female of $TL < 70$ cm (see Appendix A3).
$\phi_{jt}$	Fishing	Derived from a lognormal	Probability that a juvenile does not survive fishing. Based on a full recruitment model, $\phi_{jt} = 1 - e^{-F_{jt}} = 1 - e^{-q_j E_t}$ , relates the annual fishing mortality rate for juveniles, $F_{jt}$ , with the catchability, $q_j$ , and the annual standardized fishing effort, $E_t$ . Insufficient knowledge on the fishery leads us to admit a vague lognormal as the prior distributions for $q_j$ . A crude estimate of its expected value was calculated using successively a Beverton and Holt (1957) model, to obtain a guesstimate of the annual mortality rate $Z$ , and then the relations $F = Z - M_{bja}$ and $E[q_j] = -F \bar{E}$ , where $\bar{E}$ is the effort mean value.
$\phi_{at}$	Fishing	Derived from a lognormal	Probability that an adult does not survive fishing. The above procedure was used.

with parameters  $\Theta = (\phi_S, C_b, C_j, p_B, \phi_j, \phi_a, \psi)$  and

$$g_t(\mathbf{n}_t | \mathbf{n}_{t-1}; \Theta) = \int_{\mathbf{u}_t^f} \int_{\mathbf{u}_t^b} \int_{\mathbf{u}_t^c} \int_{\mathbf{u}_t^s} g^S(\mathbf{u}_t^S | \mathbf{n}_{t-1}; \Theta) g^C(\mathbf{u}_t^C | \mathbf{u}_t^S; \Theta) g^B(\mathbf{u}_t^B | \mathbf{u}_t^C; \Theta) g^F(\mathbf{n}_t | \mathbf{u}_t^B; \Theta) d\mathbf{u}_t^F d\mathbf{u}_t^S d\mathbf{u}_t^T d\mathbf{u}_t^B.$$

The estimation of the parameters and states is done within the Bayesian paradigm, implying non-trivial integration of several probability density functions, accomplished through sequential Monte Carlo methodology. This methodology allows sampling from the desired posterior distributions by sampling values from other conveniently chosen distributions and then reweighing them properly. More specifically, we chose to perform sequential importance sampling with resampling and kernel smoothing, a technique developed for this kind of state space models, implementing the algorithm and the guidelines for its tuning proposed by Liu and West (2001).

### 2.3 Model parameters and prior distributions

The prior distributions for the parameters in the model were selected in a way that each of them incorporates as much information as is available for the species. A description of all the subprocess parameters is given in Table 1. The variances of all the beta distributions for the probability parameters were determined to be the maximum possible values that still allow proper distributions (area under the density curve equal to one). This procedure was adopted since the information on the variance of these parameters is scarce, and also because the use of a large variance can balance the unknown variation associated with environmental changes, which were not considered in the model due to the paucity of observational data.

To initialize the process, the number of females fished in the first observed year,  $y_0$ , was used. Because the youngest juveniles are never fished,  $y_0$  was set equal to the sum of the total number of fishable juveniles,  $N_{j0}$ , plus the total number of adults,  $N_{a0}$ , weighted by the corresponding fishing



probabilities at the year 0,  $N_{a0} \times \phi_{a0} + N_{j0} \times \phi_{j0} = y_0$ . If  $p_a$ ,  $p_j$  and  $p_{nr}$  designate the fraction of adults, fishable, and non-fishable juveniles in the population respectively, the initial population dimension can be calculated by  $N_0 = y_0 / (p_a \phi_{a0} + p_j \phi_{j0})$  and  $\mathbf{n}_0 = N_0(p_{nr}, (1 - \phi_{j0})p_j, (1 - \phi_{a0})p_a, \phi_{j0}p_j, \phi_{a0}p_a)$ . Beta distributions were assumed for  $p_j$  and  $p_a$ , whose expected values were estimated according to the rationale adopted for the estimation of the probabilities of class transition.

To study the sensitivity of the model estimates to the prior distributions, three scenarios were considered. In the first scenario, informative priors based on the estimates referred to above were assumed for all the parameters. In the second scenario, all the parameters' prior distributions were non-informative. The third scenario was similar to the second except for the  $p_B$ , whose distribution was the same as in the first scenario.

The catch estimates for the year  $t$ ,  $\widehat{Y}_t$ , correspond to the median of the sums of the abundance estimates of the state process vector components representing the juveniles and the adults fished in each iteration. The estimates of the abundance of specimens in the year  $t$  are derived in the same way but considering all the population vector components, while the estimate of non-fished specimen abundance in the year  $t$  is restricted to the juveniles not yet recruited as well as juveniles and adults that have survived to fishing in that year.

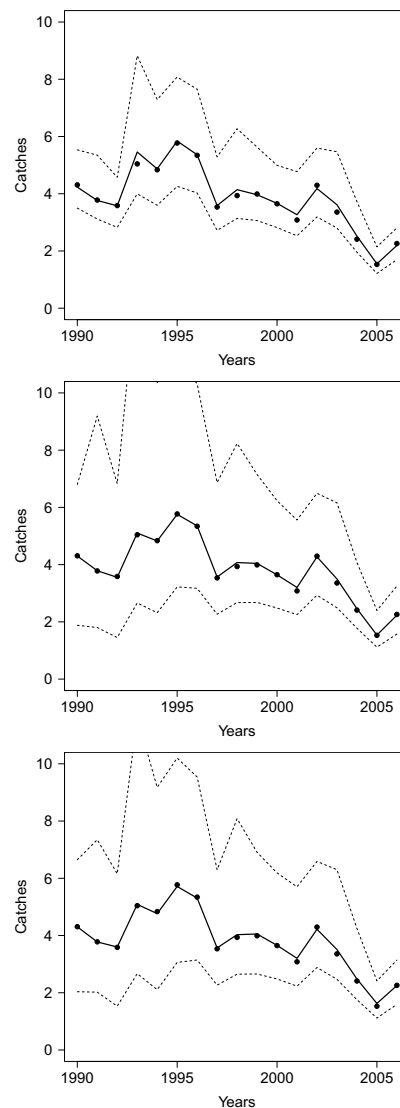
The comparison between the results for the three scenarios was completed using the expected deviance and also by visual inspection of the credible intervals. Contrarily to the confidence intervals, the latter are intervals in the domain of the posterior probability distribution.

### 3 Results

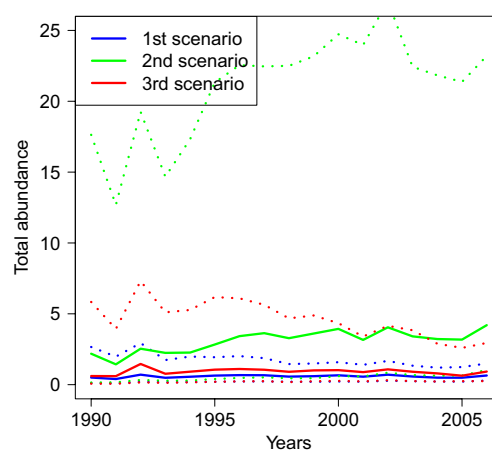
The application of the model produces annual estimates (posterior medians) for the five components of the state process vector, as well as the posterior distributions for all the parameters involved. To implement the estimation algorithm, 250 000 initial particles were used as well as a smoothing parameter (Liu and West 2001) of 0.6 (0 = maximal smoothing; 1 = no smoothing). The Monte Carlo error was evaluated by averaging the coefficient of variation for all the parameter mean estimates, based on five runs, given a value of 6.1%.

The annual catch estimates derived from the model using informative priors for the parameters and the corresponding observed values showed the best adjustment (expected deviance of 337.1). The ranges of the 95% credible intervals were relatively narrow for all the years included in the model (Fig. 1, upper panel). The results obtained for the second scenario, where only vague priors were considered, present the worst adjustment (expected deviance of 344.5) and the respective 95% credible intervals (Fig. 1, middle) were the widest, as a result of all the uncertainty admitted for the biological parameters. For the third scenario the expected deviance was 343.4, corresponding to an intermediate adjustment in between the other two scenarios. This was further supported by credible intervals narrower than in the second scenario but larger than in the first (Fig. 1, lower panel).

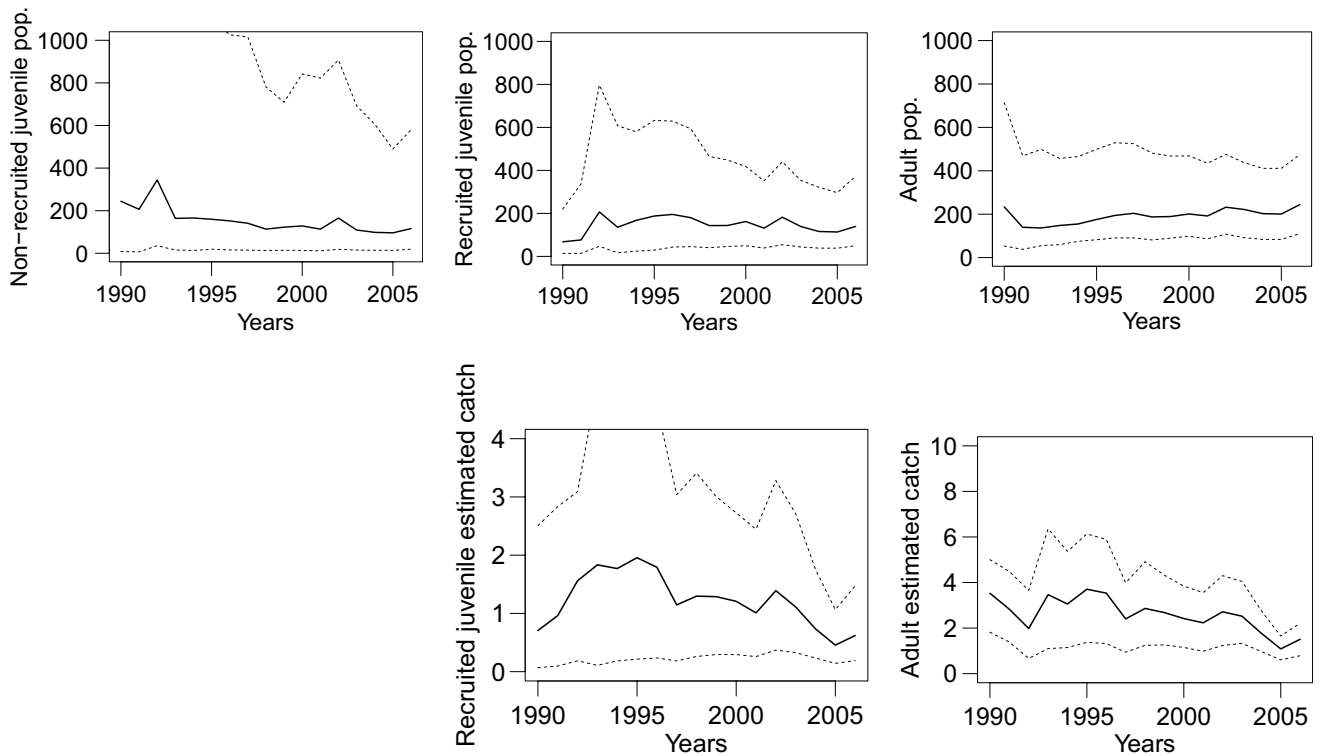
Figure 2 presents the estimates of the annual total abundance for each scenario. In the two cases where informative



**Fig. 1.** Observed female *C. coelelepis* catches in number (points) – in  $10^4$ . Estimated catches (solid line) and respective 95% credible intervals (dashed lines), for the first scenario (top), second scenario (middle) and third scenario (bottom).



**Fig. 2.** Estimates of the annual total abundance (in  $10^7$ ) for each of the three scenarios and their respective 95% credible intervals (dotted lines).



**Fig. 3.** Population abundance estimates (upper row) and estimated catch (lower row) in numbers ( $10^4$ ) for non-recruited juveniles (left), recruited juveniles (middle) and adults (right), for the first scenario, and their respective 95% credible intervals (dotted lines).

distributions were used, the abundance did not have a significant trend, but for the scenario where all the parameter prior distributions were vague, there was an increasing trend. Also in this case, the abundance estimates were almost three times higher than those in the other two scenarios, which were similar among themselves.

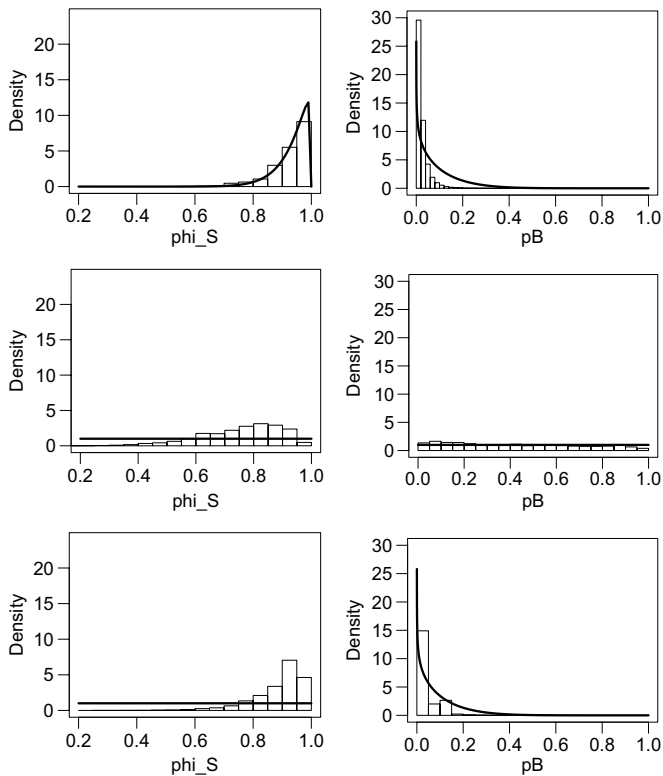
The results for the scenario using informative priors showed that in more recent years the estimated population abundance of both recruited juveniles and adults (non-fished components in the state vector) were stable (Fig. 3, upper row), while the catch of these two life stages (fished components in the state vector) decreased (Fig. 3, lower row).

The posterior distributions of the parameters differed considerably between the three scenarios. Between the first and second scenarios the major differences were associated with  $p_B$  (Fig. 4, right column) and class transition probability  $C_b$  (Fig. 5, left column), as can be seen when comparing their posterior distributions obtained for these scenarios. Although on a smaller scale, similar differences could also be noted for class transition probability  $C_j$  (Fig. 5, right column) and the surviving probability  $\phi_S$  (Fig. 4, left column). Between the second and third scenarios, the parameters  $C_b$ ,  $C_j$  and  $\phi_S$  have similar behaviour. Though their prior distributions in both scenarios are vague the posterior distributions for the third scenario approached the posterior distributions of the first scenario, where full information was given. Unsurprisingly, for the parameter  $p_B$ , the differences between the two scenarios are of the same order as those referred to in the preceding paragraph. The catchability parameters  $q_j$  and  $q_a$  have similar posterior behaviours, only presented for the latter, in Figure 6. The two last scenarios show almost identical

posterior distributions, quite different from the posterior distribution of the first scenario which, on the other hand, closely follows the prior distribution for this scenario.

## 4 Discussion

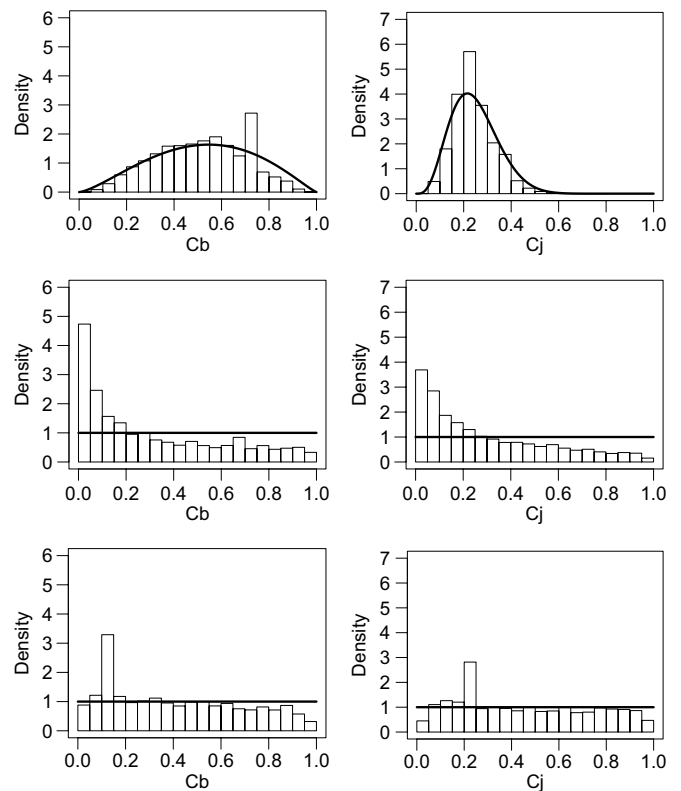
Compared with other commonly used deterministic abundance dynamic models, the approach applied in this paper has important advantages. Firstly, it combines within the same model the usual fishery data used in stock assessment models, but possibly observed with error, with information on crucial processes of the species life cycle and its reproductive potential, which are key factors for k-strategists. Moreover, the flexible way in which these processes may be included in the model enables an easy analysis of the links between different biological life settings and abundance trends. Furthermore, it has the merit of being applicable in situations where the observational data are imprecise or where knowledge about the life process parameters is poor. In the former case, large errors can be assigned to the observational process data and, in the latter case, flattened prior distributions can be chosen for the parameters. Secondly, in addition to providing abundance estimates and their respective credible intervals, this approach produces updated estimates of the parameters of the biological life cycle that can be compared with the prior knowledge. Finally, though the problem was not addressed in this paper, this approach can easily accommodate simulation-based short and medium term forecasts of the abundance beyond the observed time interval, allowing for examination of the consequences of alternative harvest policies.



**Fig. 4.** Prior (solid line) and posterior (histogram) distributions of the probability of surviving  $\phi_S$  (left) and of the probability that an embryo produces a surviving female  $p_B$  (right) for the first (upper), second (middle) and third (lower) scenarios.

Though the three scenarios analysed produced good adjustments between the observed and estimated annual catches, the best results were obtained using informative prior distributions for the biological parameters (first scenario). The second scenario, where only non-informative priors were used, produced the worst adjustment, and the third scenario, where an informative prior was adopted exclusively for  $p_B$ , presented an intermediate adjustment. It is also worth noting that the more precise information introduced in the first scenario has the effect of considerably narrowing the 95% credible intervals of the annual catches that were quite wide in the other two scenarios. In spite of that, for all three cases, the credible intervals are wider at the beginning of the time period than at the end, reflecting a high uncertainty of the fishery information and a low impact of the prior updating process in the early years.

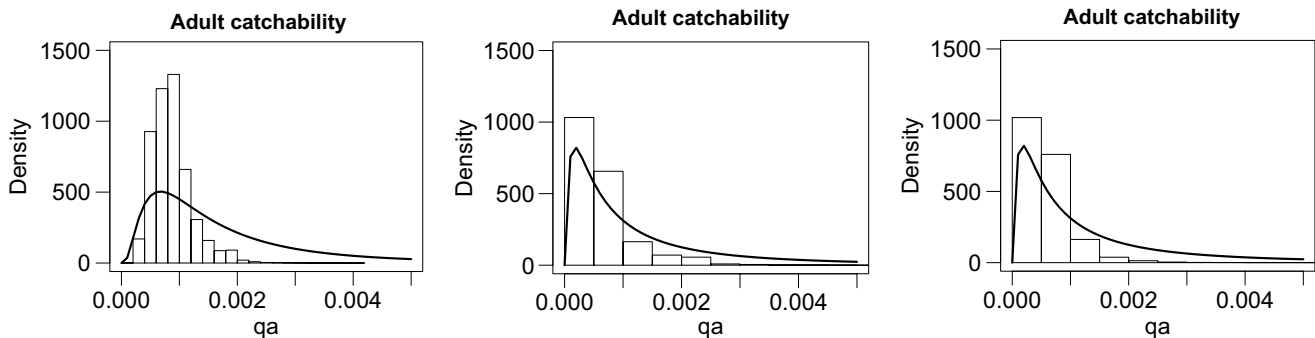
Results obtained for the posterior distributions of the three scenarios also highlight the importance of knowledge of the biology of the species, particularly its reproductive potential and growth, as well as its integration in the model through the parameters  $p_B$ ,  $C_b$ , and  $C_j$ . In the two scenarios where  $p_B$  had the same informative prior, the posterior distributions agreed with it and were quite skewed to the left, highlighting the low productivity of the species. This is associated with a low potential fecundity, also reported for this species in other geographical areas (Clarke et al. 2001; Daley et al. 2002; Girard and Du Buit 1999; Yano and Tanaka 1988), and with a long gestation time. The value adopted for the latter was a rough estimate (see Appendix A3), but similar gestation times are reported in the



**Fig. 5.** Prior (solid line) and posterior (histogram) distributions of the probabilities that a non-recruited individual transits to the juvenile stage  $C_b$  (left) and that a juvenile transits to the adult stage  $C_j$  (right) for the first (upper), second (middle) and third (lower) scenarios.

information available about other sharks (Braccini et al. 2006; McLaughlin and Morrissey 2005). Therefore, the adoption of a low potential fecundity in the prior seems to be the most important option, taking into account that it determines a long population generation time, which is universally accepted for the deep-water sharks (Simpfendorfer and Kyne 2009).

In the second scenario, where no information was given, the overall picture changed completely. The posterior distribution of  $p_B$  was weakly updated by the data and, despite presenting a small hump at the values compatible with low productivity, high values still have a large probability, bringing its mean to approximately 0.43, a value very far from that considered for the mean of the informative prior (0.09). Similar behaviour was found for the parameters  $C_b$  and  $C_j$  with posterior expected values equal to 0.71 and 0.69 respectively, much higher than the corresponding considered values for the informative prior distributions (0.53 and 0.25), indicating that, in the non-informative setting, the growth is faster than in the first and third scenarios. These results somewhat contradict the low growth rate accepted for the *C. coelolepis* (Moura 2011) and other related species (Clarke et al. 2002; Irvine et al. 2006) which were confirmed by the expected values of the posterior distributions of these two parameters in the all-informative scenario (0.51 and 0.24). The posterior mean of the survival probability parameter varies in the opposite direction, in this case 0.75, a value considerably lower than the mean for the informative prior distribution (0.936). All of these results for the second scenario indicate that when no information is given



**Fig. 6.** Prior (solid line) and posterior (histogram) distributions of the adult catchability parameter  $q_a$  under the first (left), second (middle) and third (right) scenarios.

to the model, the available data is not enough to bring down the estimate of the parameter  $p_B$ , and all the estimates drive toward an equilibrium that would be suitable for a much more productive species with a faster growth rate, which implies a greater natural mortality. These are characteristics of shallower species that presents high abundance levels and, indeed, it was what was found in this case for the total abundance estimates of the *C. coelolepis*. This second scenario placed the population abundance at a much higher level than the other two (that were quite close to each other), though in the third scenario precise information was only given on the parameter  $p_B$ . In this case, it is sufficient to give information on only this parameter to get the model to reach an equilibrium close to the one of the first scenario (which is much more compatible with this deep-water species life history). The leading role of  $p_B$  is in agreement with the importance of the reproductive output in the elasmobranch dynamics, particularly in viviparous species.

Considering results connected with the juvenile and adult classes, it can be said that the impossibility of separating the observational data between these two classes has some setbacks. The information contained in the data restricted to the total catches was insufficient to update the distributions of the parameters related to these two classes, specifically the prior distributions for the catchability parameters, whose function is to measure the interaction between the resource and the fishing effort (Gulland 1983). This can also be a consequence of the use of the simplest catchability model derived from the Baranov catch equation which may not accurately reflect the relationship between fishing mortality and effort. Additionally, it is known that anthropogenic, environmental, biological, and management processes may drive changes in catchability over time (Hannesson 1983; Robins et al. 1998; Skjold et al. 1996). This temporal variability was not considered in the present approach since there were no signs of change on the fishing regime and no new management measures were adopted.

The estimated abundance trends for both juveniles and adults in recent years contrasts with the decrease in the estimated catch-in-number of these stages. These trends may simply reflect the response of the population to the decline of the fishing effort lately, which may be a consequence of the restrictions on the fishing activity adopted by the European Commission (EC) specifically for the deep-water sharks. In 2005 the EC introduced an emergency temporary ban on all gillnet fishing at depths below 200 m in ICES

Divisions VI and VIIb-k and Subarea XII east of 27°W (EC Regulation No. 51/2005). The EC management measures were later revised and, since 2006, include a permanent ban on all deep-water gillnet fisheries at depths below 600 m, effectively closing fisheries for deep-water sharks, mainly *C. coelolepis* and *C. squamosus* (EC Regulation No. 41/2006). Since 2009, the EU total allowable catch for most deep-water shark species has been set to zero (EC 1359/2008 and EC 1225/2010).

The results of the present application of a Bayesian state space model suggest the following conclusions: taking into account the main biological drivers together with the fishing information in the same model provides a coherent picture linking the *C. coelolepis* population abundance trends off mainland Portugal with the species' life history parameter estimates. Although the available information on the fishery was scarce and did not include separated catch data for juvenile and adults, the model was capable of estimating the abundances of these life stages. This result is particularly interesting since the abundance estimates based on standardized CPUE do not offer any information on this. Finally, it is also important to point out that the abundance trajectory of these life stages is in line with the overall abundance trend already presented in the beginning of this section, supporting the conclusion that this particular *C. coelolepis* population does not seem to have been greatly affected by the fishery. Furthermore, this model is flexible enough to be applied, with some fine-tuning, to the estimation of the abundance trends in other populations, provided that there is some information on the life cycle history of the species under analysis.

## Appendix A1

The prior distribution for the probability of class transition  $C_b$  is assumed to be a beta distribution, with parameters determined in accordance with knowledge on species growth.

The expected value  $E[C_b]$  was calculated according to the following steps: First, the range of length classes within which non recruited juveniles are likely to transit to the juvenile group in one year was calculated and, second, the probability that a specimen belongs to that range of lengths was also calculated.

For the first step, species growth was assumed to follow a Von Bertalanffy model (Cailliet et al. 2006). The parameters of the model were determined by Moura (2011) as  $k = 0.007$  and



$L_{\infty} = 128.4$  cm, which was calculated based on the assumption that the maximum observed length, 122 cm, corresponds to 95% of  $L_{\infty}$ .

During one year, the expected change in specimens belonging to a 1-cm length class centered on  $l$  is given by  $(L_{\infty} - l)(1 - e^{-k})$ , Quinn et al. (1983). Based on this, non recruited juveniles with sizes included in the length interval [65 cm, 70 cm] are likely to grow and transit to the juvenile group.

The second step included the determination of the probability of a non recruited juvenile to belong to the length interval [65 cm, 70 cm]. This probability was calculated based on the female length distribution of the Portuguese dogfish determined by adjusting a normal model to survey data available on Clarke et al. (2005). The obtained value of 0.53 was considered to be the expected probability of class transition  $C_b$ .

## Appendix A2

For the prior distribution for the probability of class transition  $C_j$ , the expected value is  $E[C_j]$  and is determined using the same procedure used for  $E[C_b]$ . In this case, specimens belonging to the juvenile fishable stage with sizes included in the length interval [98 cm, 101 cm] are expected to transit to the adult group. The expected probability of class transition of  $C_j$  was estimated as 0.25.

## Appendix A3

The probability that an embryo produces a surviving female in one year follows a beta distribution. The expected value of this distribution was calculated as  $E[p_B] = \bar{F}/f$ , where  $\bar{F}$  is the mean number of the annual newborn females that have survived from each pregnant female and  $f$  is the maximum of the uterine fecundity (number of embryos per pregnant female). Estimates of the above reproductive parameters are based on knowledge of the species fecundity and on the fact that the average number of embryos in the uterus does not change with the size of female, ovulation is synchronous, and embryos from one litter are of the same age.

The mean of uterine fecundity,  $\bar{F}$  and its standard deviation was calculated as  $11.3 \pm 3.9$  embryos per pregnant female, the sex ratio at birth was 1:1, and the proportion of pregnant females among mature females (i.e. females capable of reproducing) in each year is 0.54 (Figueiredo et al. 2008).

From these values, the maximum uterine fecundity was determined as  $f = 15 \approx 11.31 + 3.93$ , and the annual average number of surviving newborn females per each adult female was,  $1.4 \approx 11.31 \times 0.5 \times 0.54/2.17$ , where 2.17 years  $\sim$  26 months is the average duration of the embryonic development. As  $1.4 = 15E[p_B]$ , the estimated value of  $E[p_B]$  is 0.0935.

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