



A Bayesian model for anchovy (*Engraulis encrasicolus*): the combined forcing of man and environment

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ABSTRACT

Fishery collapses frequently result from combined pressures of the environment and man, which are difficult to discern because of the complexities involved and our limited knowledge. Models to resolve this complexity often become too sophisticated, with too many assumptions and, consequently, with little capacity to predict beyond calibration data. In this paper we implement a different procedure where the model is kept simple and uncertainty accounts for the equation imperfectness to reproduce ecological complexity. Human and environmental forcing on an anchovy (*Engraulis encrasicolus*) stock are simulated with only six parameters plus their error terms, and the uncertainty is computed with Bayesian methods. The simple structure is able to reproduce the major dynamical features of this species in the Gulf of Cádiz, including data on life stages and age structure that had no contact with the model. This is a distinct performance for a frugal approach working on a mid-trophic species and a positive instance where parsimony can simulate the interaction of man, fish and the environment, provided uncertainty is accounted for in the process.

Key words: anchovy, anthropogenic forcing, Bayesian model, environmental forcing, Gulf of Cádiz, life cycle

INTRODUCTION

Fishery collapses frequently result from the combined pressure of the environment and man. Although fish populations fluctuate in the absence of human activity (Baumgartner *et al.*, 1992), fishing pressure increases vulnerability to collapse (Cushing, 1996; Bakun and Weeks, 2006), in particular when combined with an adverse physical environment (Ruiz *et al.*, 2007). Short-lived pelagic species such as clupeoids are very sensitive to their physical environment (Nakata *et al.*, 2000; Lloret *et al.*, 2001; Guisande *et al.*, 2004; Erzini, 2005; Basilone *et al.*, 2006) as it affects the survival of their early life stages and may cause recruitment failures (Cingolani *et al.*, 1996; Dimmlich *et al.*, 2004). Mechanistic theories merge physical (transport, turbulence, etc.) and biological (predation, growth, etc.) components to connect environmental fluctuations with clupeoid recruitment (Parrish *et al.*, 1983; Checkley *et al.*, 1988; Cury and Roy, 1989; Bakun, 1996; Bakun and Broad, 2003). Hydrodynamic processes retain (advect) early stages within (from) favourable conditions. Adequate temperature and food availability enhance growth rates and reduce characteristic acute mortality owing to predatory pressure and starvation. Hence, marine areas optimal for the successful recruitment of clupeoids frequently have slow currents, high primary production and warm waters (Cole and McGlade, 1998).

The shelf zone between Capes Santa María and Trafalgar in the Gulf of Cádiz embraces these favourable features and sustains a significant fishing activity, anchovy (*Engraulis encrasicolus*) being one of the main resources. Bathymetry and coastline create a cyclonic circulation segregated from the energetic currents nearby the Strait of Gibraltar (García-Lafuente *et al.*, 2006). Salt marshes and river input respectively heat and fertilize the shelf during summer, generating a large pool of warm and chlorophyll-rich water (Navarro and Ruiz, 2006; García-Lafuente and Ruiz, 2007). At that time of year the concentration of fish eggs and larvae is very high (Baldó *et al.*, 2006), particularly for anchovy (Ruiz *et al.*, 2006). Besides favourable conditions for planktonic stages, the shelf is connected to the lower reaches of the Guadalquivir

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Received 15 April 2008

Revised version accepted 10 November 2008

River, a nursery area for post-larvae of anchovy (Baldó and Drake, 2002; Drake *et al.*, 2007).

Favourable conditions for anchovy recruitment are distorted under specific meteorological regimes at the southern Iberian Peninsula. Shelf currents are highly sensitive to easterly winds, which blow as intense bursts in the area. Persistent easterlies cause the off-shore spilling of waters from the shelf through Capes Santa María and San Vicente (Relvas and Barton, 2002). Westward advection of fish larvae under this regime has been documented (Catalán *et al.*, 2006). In addition, latent heat fluxes during easterlies cool shelf waters and hamper anchovy spawning (Ruiz *et al.*, 2006). Rain at the south of the Iberian Peninsula fertilizes the shelf through freshwater discharges from the Guadalquivir River (Navarro and Ruiz, 2006). A dam, 110 km upstream from Guadalquivir mouth, tightly regulates discharges, which are dramatically reduced during years of severe drought. Besides lowering the primary production of the shelf, the agriculture management of the dam during dry years modifies the seasonal pattern of discharges and negatively impacts the anchovy nursery within the estuary (Drake *et al.*, 2002).

Low recruitment under adverse meteorology, intense easterlies and low precipitation, is thought to decrease anchovy landings at the Gulf of Cádiz (Ruiz *et al.*, 2006). Although similar features are also observed in other anchovy fisheries (Motos *et al.*, 1996), they are seldom included in management models (Freon *et al.*, 2005). Lack of an underlying hypothesis and neglect of inferences from data are among the flaws leading to this failure to connect fisheries assessment and ecosystem functioning (Barange, 2001). In addition, uncertainty owing to imperfect model representation of recruitment and its connection with the environment is barely accounted for in these approaches. Uncertainty is a key component to compute in the implementation of any science aimed at supporting decision-making (Lindley, 1971). When applied to fishery research, Bayesian approaches compute this uncertainty as a natural output after application of Bayes' theorem (Punt and Hilborn, 1997). Implementation of state-space schemes of stock dynamics under the Bayesian approach accounts for both observational and hypothesis uncertainty (Meyer and Millar, 1999; Rivot *et al.*, 2004). As a result, they elude the dichotomy between mechanistic (e.g., Fasham-like ecosystem models) and purely data-driven (e.g., generalized additive models) inference techniques in addition to assimilating all available information to reduce uncertainty. This is particularly useful when connecting information sources with

different origin and format as are available for small pelagic fisheries. For a small pelagic like anchovy, the Bayesian approach straightforwardly applies these different sources to provide consistent simulation of stock dynamics as well as projections of future scenarios (Ibaibarriaga *et al.*, 2008).

Available knowledge of stock dynamics may include hypotheses concerning recruitment and its interaction with the environment but also fishery data of varying quality and resolution as well as estimates of the stock by acoustic or other fishery-independent methods. The former involves latent variables (*sensu* Congdon, 2006; i.e., state variables that drive the dynamics of the model but cannot be observed; e.g., spawning, recruitment or stock size) and accurate measurements (e.g., wind, rain, currents, etc.) interconnected by processes consistent with an underlying hypothesis where the environment forces population dynamics. Therefore, error sources come from an imperfect hypothesis or its inadequate mathematical representation. The latter involves errors both in the observations and in the model connecting these with the latent variables, e.g., catch per unit effort is less accurately measured than water temperature and its connection with stock size frequently assumes a constant catchability. The Bayesian approach easily and consistently accommodates this disparity of knowledge (e.g., hypothesis versus data, records of different accuracy or frequency, observations connected to latent variables) when modelling the dynamics of small fish.

This paper implements this approach for a state-space model of anchovy life stages. The model is used to infer 17 years of stock size in the Gulf of Cádiz. As this anchovy stock has proven to be sensitive to favourable and adverse environmental conditions (Ruiz *et al.*, 2006), its population dynamics is modelled under the influence of the physical environment and connected to available observations of sea surface temperature, river discharge, wind, catches, catch per unit effort, and acoustic records, as available. The model diagnoses values that are consistent with independent observations of anchovy early life stages in the Gulf of Cádiz. It is also able to explain the main crises historically recorded for this fishery in the region.

MODEL

Process model

The model is applied for the 204 months between January 1988 and December 2004. Anchovy abundance at various life stages is estimated at this monthly

resolution to the maximum age of 24 months. Anchovies of the 2+ year group are very rarely observed in the fishery (Anonymous, 2006) and are not included in the model. Therefore, the model considers 0, 1, 2, ..., and 23 monthly age groups. The first age group (0) is considered eggs (H) and the second, larvae (L).

Spawning peaks in May–June, and in March–April of the next year most of the population is already mature (Millán, 1999). On that account, eggs are introduced in the model as a proportion of the biomass of individuals beyond age group 9, $\sum R$, provided the water is warmer than 16°C and the temperature (T) has increased at least 1° in the last month. This approach follows other attempts to model the population dynamics of *Engraulis encrasicolus* where egg production is proportional to reproductive biomass with a factor that accounts for the proportion of females in the population, the biomass invested by them in the production of eggs, and the proportion of that biomass resulting in healthy eggs (Oguz *et al.*, 2008). Equation 1 summarizes all these factors into a single parameter (α , see Tables 1 and 2 for model nomenclature and life-stages respectively) whose *a posteriori* probability distribution is obtained after implementation of the Bayesian approach. Limiting egg production to time periods when a minimum temperature is obtained and to the warming phase of the seasonal cycle follows observations made for this species (García and Palomera, 1996; Motos *et al.*, 1996) and particularly for

Table 2. Life stages considered in the model.

Age (months)	Stage
0–1 (0)	H (egg)
1–2 (1)	L ¹ (larvae 1st month)
2–3 (2)	L ² (larvae 2nd month)
3–4 (3)	J ¹ (juvenile 1st month)
4–5 (4)	J ² (juvenile 2nd month)
5–6 (5)	J ³ (juvenile 3rd month)
6–7 (6)	Y ¹ (young 1st month)
7–8 (7)	Y ² (young 2nd month)
8–9 (8)	Y ³ (young 3rd month)
9–10 (9)	R ¹ (reproductive 1st month)
10–11 (10)	R ² (reproductive 2nd month)
...	...
23–24 (23)	R ¹⁵ (reproductive 15th month)

its spawning in the Gulf of Cádiz (Ruiz *et al.*, 2006). The state equation for eggs is:

$$\bar{H}_t = \alpha \sum R_t \quad \text{if } T_t > 16 \text{ and } (T_t - T_{t-1}) > 1, \\ \text{or } 0 \text{ otherwise.}$$

$$H_t \sim N(\bar{H}_t, S_H) \quad (1)$$

N stands for the normal distribution of egg abundance at month t (H_t) with mean and standard deviation (accounting for process error) equal to \bar{H}_t and S_H , respectively.

Table 1. Symbols for the parameters and variables implemented in the model.

Symbol	Description	Units	Prior
α	Parameter for egg inputs	Month ⁻¹	Normal
ρ	Parameter for the effect of discharges	Month ⁻¹	Normal
τ	Parameter for the effect of sea temperature	°C ⁻¹	Normal
λ	Parameter for the effect of easterlies	Day ⁻¹	Normal
μ	Residual mortality after fishing and environmental (temperature, wind and discharges) losses	Month ⁻¹	Normal
q	Catchability	Fishing trips	Normal
S_H	Standard deviation of egg input process model	n	Gamma
S_L	Standard deviation of larval survival process model	n	Gamma
S_J	Standard deviation of juvenile survival process model	n	Gamma
S_{YR}	Standard deviation of young and reproductive survival process model	n	Gamma
S_{CPUE}	Standard deviation of CPUE observational model	Tons/fishing trip	Gamma
S_A	Standard deviation of acoustics observational model	n	Gamma
CPUE	Catch per unit effort	Tons/fishing trip	
A	Acoustic estimate of stock size	n	
C	Catches of anchovy in the Gulf of Cádiz	n	
T	Sea surface temperature	°C	
D	Monthly discharges from Alcalá del Río dam	hm ³	
W	Days per month with easterlies >30 km h ⁻¹	Days	

Larval survival is controlled by the intensity of easterlies, due to its potential to advect the larvae away from favourable conditions in the shelf zone (Catalán *et al.*, 2006; Ruiz *et al.*, 2006). This survival is also considered to improve with increased temperatures because less time is needed to grow and, as a consequence, predation can be avoided more (Regner, 1985). The state equation for the first stage of larvae is:

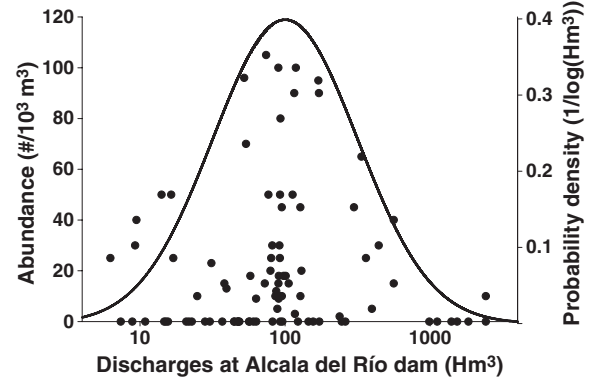
$$\begin{aligned} \bar{L}_t^1 &= (1 - e^{-\tau T_t}) e^{-\lambda W_t} H_{t-1} \\ L_t^1 &\sim N(\bar{L}_t^1, S_L) \end{aligned} \quad (2)$$

where T_t and W_t are respectively the average sea surface temperature in the shelf and the time (number of days) that strong easterlies ($>30 \text{ km h}^{-1}$) have blown during the month number t . Parameters τ and λ modulate thermal and wind effects, respectively. As for α , their *a posteriori* probability distribution is obtained after implementation of the Bayesian approach. \bar{L}_t^1 and S_L are the mean and standard deviation (accounting for process error) of larval abundance.

In the second larval stage (\bar{L}_t^2) are individuals of the month 2 age group with sizes above 3 cm. They are post-flexion larvae, although still undergoing metamorphosis (Arias and Drake, 1990) and have a certain swimming capacity but not fully enough to control their horizontal position in the shelf, where currents are of the order of tens of centimetres per second (Sánchez *et al.*, 2006). Following this limited motility, anchovy of this size can be found inside the Guadalquivir River estuary, although in lower numbers than the massive appearance of larger sizes (Drake *et al.*, 2007). Their survival is, therefore, conditioned by a mixture of the physical environment on the shelf (wind and temperature) and in the estuary (freshwater regime).

Survival of anchovy early life stages in the estuary is connected to the freshwater regulation in the dam of Alcalá del Río (Drake *et al.*, 2002). Lack of discharge (D_t) implies lack of fertilization and low production of the estuary with less food for anchovy early stages. Excessive discharges, conversely, lower the salinity to unsuitable values for anchovy, and individuals leave the estuary or die (Fernández-Delgado *et al.*, 2007). Figure 1 shows the abundance of anchovy early stages in the estuary versus discharges from Alcalá del Río. Variability is high because the data mixes seasons when early stages are abundant because of the reproduction cycle (e.g., mid-summer) with periods when they are not (e.g., early spring). However, maximum values are enveloped within the standardized normal

Figure 1. Concentration of anchovy at post-larval stage as a function of monthly discharge from the Alcalá del Río dam. The solid line is the function $\Phi(2(\log(D)-2))$, where Φ is the probability density function for the standardized normal. Data derived from Drake *et al.* (2007).



function $\Phi(2(\log(D_t) - 2))$, which identifies the highest abundances achievable at the estuary for a given discharge. This feature is used to model the influence of discharge on the survival of anchovy stages. As explained above, for the second larval stage this influence is mixed with that of the physical environment on the shelf and modelled as:

$$\begin{aligned} \bar{L}_t^2 &= \rho(1 - e^{-\tau T_t}) e^{-\lambda L_t} \Phi(2(\log D_t - 2)) L_{t-1}^1 \\ L_t^2 &\sim N(\bar{L}_t^2, S_L) \end{aligned} \quad (3)$$

where ρ makes survival proportional to Φ .

The next stages are individuals of age group 3, large enough to move into the estuary. Anchovy of this and larger sizes appear in large numbers within the estuary until they are about 7 cm and leave for open waters (Drake *et al.*, 2007). The growth equation of von-Bertalanffy applied to the anchovy of the Gulf of Cádiz (Bellido *et al.*, 2000) assigns this to size five individuals. Accordingly, juvenile stages are modelled as:

$$\begin{aligned} \bar{J}_t^1 &= \rho \Phi(2(\log D_t - 2)) L_{t-1}^2 \\ \bar{J}_t^i &= \rho \Phi(2(\log D_t - 2)) J_{t-1}^{i-1} \quad \text{for } i = 2 \text{ and } 3 \\ J_t^i &\sim N(\bar{J}_t^i, S_j) \quad \text{for } i = 1, 2 \text{ and } 3 \end{aligned} \quad (4)$$

When juveniles leave the estuary, they swim enough to avoid adverse environments and survival of stages beyond 5 is therefore assumed to be independent of physical conditions. They also leave the estuarine protection from predation and fishery

exploitation (Drake *et al.*, 2007). The former loss is included as a mortality term represented as parameter μ whose *a posteriori* probability distribution is obtained after implementation of the Bayesian approach. Fishery losses are obtained from ICES landing data for the region IX.a south and considered to be proportional to the relative abundance of that stage to the total of individuals larger than the 5 age group ($\sum B_t$). As Equation 5 shows, the resulting algorithm is equivalent to considering fishing mortality constant through ages. Although effort is frequently higher for larger (older) individuals of other fisheries, there exists no information on this selectivity for anchovy in the Gulf of Cádiz. No clear *a priori* age-selection pattern seems to be expected for a fishery where the negligible abundance of group 2 narrows the window of captured sizes and the market does not particularly appreciate larger individuals over smaller ones.

$$\begin{aligned}\bar{Y}_t^1 &= (1 - \mu) \left(1 - C_{t-1} / \sum B_{t-1}\right) J_{t-1}^3 \\ \bar{Y}_t^i &= (1 - \mu) \left(1 - C_{t-1} / \sum B_{t-1}\right) Y_{t-1}^{i-1} \quad \text{for } i = 2 \text{ and } 3 \\ \bar{R}_t^1 &= (1 - \mu) \left(1 - C_{t-1} / \sum B_{t-1}\right) Y_{t-1}^3 \\ \bar{R}_t^i &= (1 - \mu) \left(1 - C_{t-1} / \sum B_{t-1}\right) R_{t-1}^{i-1} \quad \text{for } i = 2 \text{ to } 15 \\ Y_t^i &\sim N\left(\bar{Y}_t^i, S_{YR}\right) \quad \text{for } i = 1, 2 \text{ and } 3 \\ R_t^i &\sim N\left(\bar{R}_t^i, S_{YR}\right) \quad \text{for } i = 1 \text{ to } 15\end{aligned}\quad (5)$$

where \bar{Y}_t^i and \bar{R}_t^i are respectively the mean of young ($6 < \text{age} < 10$) and reproductive (age > 9) stages of anchovy outside the estuary. S_{YR} is the standard deviation accounting for process error.

The normal distributions in Equations 1–5 were restricted to the positive domain while sampling the posterior probabilities with Gibbs techniques (see below). This follows the logical lack of negative values for the abundance of individuals.

Observational model

The model connecting the observations to the latent variables (life stages of the process model) assumes that catch per unit effort (CPUE) equals stock size ($\sum B_t$) divided by a catchability coefficient (q):

$$\overline{CPUE}_t = \sum B_t / q$$

$$CPUE_t \sim N(\overline{CPUE}_t, S_{CPUE}) \quad (6)$$

where S_{CPUE} is the standard deviation accounting for errors in the observation of CPUE data. The model assumes a proportionality between CPUE and stock abundance with a coefficient, q , that does not vary over time. Changes in fleet efficiency or dynamics, species targeting and environment variability among other factors may cause q to vary over the exploitation history of a fishery (Maunder *et al.*, 2006). In addition, school dynamics of small pelagics may result in density-dependent catchabilities (Fréon and Misund, 1999) and produce nonlinear connections between CPUE and the stock in a dynamics conditioned by vessel type (Bertrand *et al.*, 2004; Parente, 2004). These components may have limited impact on q variability for a stock such as anchovy in the Gulf of Cádiz that is spatially constrained to a small area and for a CPUE data set (see below) based on a homogeneous fraction of the purse-seine fleet. Still, q has most probably differed from constancy in a time span where the fleet has undergone a process of significant modernization and in a scenario where stock collapses and societal conflicts are present. However, lack of detailed information about the fleet as well as scarce fishery-independent data on the stock prevented us from time-resolving q variability. We rather allow the unresolved dynamics to be part of the uncertainty accounted for by the model.

ICES data (Anonymous, 2006) provide acoustic estimates of the stock size (A) for the June of years 1993 and 2004. These are included in the observational model as:

$$\begin{aligned}A_t &\sim N\left(\sum B_t, S_A\right) \quad \text{for } t = 66 \text{ and } 198 \text{ (June 1993} \\ &\quad \text{and 2004, respectively)}\end{aligned}\quad (7)$$

where S_A is the standard deviation accounting for errors in the observation of the acoustic estimates. Preliminary tests (not shown) showed little sensitivity of the model output to the inclusion of a ‘catchability’ parameter for acoustic data (i.e., to formulate the observational model for acoustic as Equation 6 rather than 7). Therefore, the simpler Equation 7 was preferred to save one parameter in the model implementation.

Directed acyclic graph

A directed acyclic graph (DAG) representation of the model is shown in Fig. 2. Following Millar and Meyer (2000), hollow and solid arrows represent logical functions and stochastic dependencies,

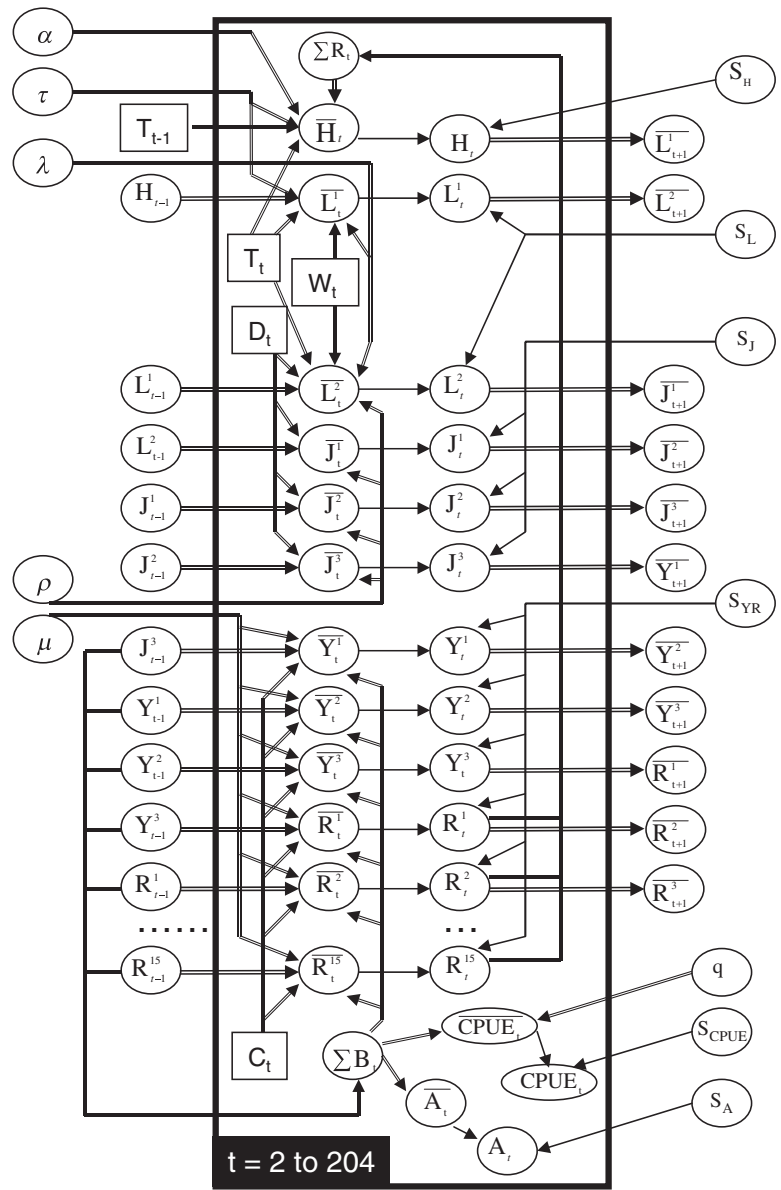


Figure 2. Directed acyclic graph of the model. Hollow and solid arrows represent logical functions and stochastic dependencies respectively. Data are represented as rectangles and oval nodes represent stochastic variables. Structures of the state-space model that is repeated from month 2 to 204 are enveloped within the heavy-line rectangle.

respectively. Data are represented as rectangles whereas oval nodes represent stochastic variables. Structures of the state-space model that are repeated from month 2 to 204 are enveloped within the heavy-line rectangle. The different stages H_t , L_t^1 , L_t^2 , J_t^1, \dots correspond to 0, 1, 2, 3, ... (see Table 2) monthly age groups, respectively. Despite its apparent complexity, the DAG incorporates the effect of the environment on the dynamics of 24 life stages of anchovy during 204 months and connects it with observations using only six parameters (α , τ , λ , ρ , μ and q) plus sources of errors (S_H , S_L, S_J , S_{YR} , S_{CPUE} and S_A).

Prior probability distributions

Conditional independence of state-space models demands that priors for the parameters (α , τ , λ , ρ , μ and q), the errors ($S_H, S_L, S_J, S_{YR}, S_{CPUE}$ and S_A), and for the first month of the state variables ($H_1, L_1^1, L_1^2, J_1^1, \dots$) be declared. It is commonly recommended to make use of available information to define priors in stock assessment (Punt and Hilborn, 1997; Hilborn and Liermann, 1998), although there is frequently criticism of altering objective inference.

We follow the rationale of Millar and Meyer (2000) and use non-informative priors for the errors and

diffuse normal distributions for the first month of the state variables. As in Millar and Meyer (2000), the inverse of error priors were approximated by Gamma (0.001, 0.001) functions to avoid improper distributions. Normal distributions for the initial priors of eggs, larvae-juveniles and young-adults are, respectively, $N(1000,10000)$, $N(100,1000)$ and $N(10,100)$, where mean and standard deviation are millions of individuals.

All parameters were restricted to positive values as the sign of the process is already made explicit in Equations 1–7. Little *a priori* information can be derived from the values of environmental parameters in the model (τ , λ and ρ) except for the qualitative knowledge that the environment modulates recruitment (Ruiz *et al.*, 2006). This knowledge was translated into priors as normal distributions with standard deviation equal to a mean (0.5°C^{-1} , 0.15 days^{-1} and 0.1 month^{-1} for τ , λ and ρ , respectively) whose value significantly modifies the survival for the average value of the environmental variable (e.g., the product of the mean λ and the monthly average of easterlies duration results in a factor of $\sim e^{-1}$ for the wind).

Similar diffuse normal distributions were also given to q , μ and α . It is not straightforward to assign a prior mean to a parameter such as μ , the residual mortality after environmental effects and fishery catches. It was then decided to explore its domain (from 0 to 1) with three values (0.01, 0.5 and 0.99). A parallel procedure was implemented for α and q . The domain of α was enclosed between zero and a (unrealistically high) top where females spawn every 2 days during 1 month with an exceptionally high batch fecundity of 40 000 eggs (Motos, 1996) that are all viable as input to the model. Similarly, the domain of q was generously constructed after considering that its value in Equation 6 can be thought (only in the algorithm world) as the number of fishing trips necessary to deplete the stock. This produces a minimum value of 1 (one trip captures the stock) and a maximum of about 10^7 (each fishing trip only captures 1 kg of anchovy). The singularities of anchovy in the Gulf of Cádiz, heavy environmental control and reduced life span (Ruiz *et al.*, 2007), prevented us from defining a prior for q from information of other fisheries (Hilborn and Liermann, 1998). This preliminary exploration of model behaviour showed little sensitivity of the parameter posterior to the point of the domain explored in the prior, except for the case of q . When values of q chosen were too small, the prior prevents high values of the posterior, whereas avoiding these small ranges

of values results in about the same posterior mean and variance. Given our lack of prior knowledge for q , we avoided this small end range of prior values for q .

Sampling the posterior probabilities of the parameters

The Bayesian approach estimates the parameters by updating their *a priori* probability with the likelihood of the observations. Bayes' theorem makes the *a posteriori* probability of the parameters proportional to the product of the priors and the likelihood:

$$\begin{aligned} \text{POSTERIORI} \propto & p(\alpha, \tau, \lambda, \rho, \mu, q, S_H, S_L, S_J, S_{YR}, \\ & S_{CPUE}, S_A, H_1, L_1^1, L_1^2, J_1^1, \dots, R_1^{15}) \times p(A_{66}, A_{198}, \\ & CPUE_1, \dots, CPUE_{204} | \alpha, \tau, \lambda, \rho, \mu, q, S_H, S_L, S_J, \\ & S_{YR}, S_{CPUE}, S_A, H_1, L_1^1, L_1^2, J_1^1, \dots, R_1^{15}) \quad (8) \end{aligned}$$

Explicit formulation of this joint probability density function is extremely laborious because of the need to construct the full conditional of a stage-resolving model with 24 states and 204 time steps. We implemented the whole Bayesian model in version 1.4 of WINBUGS (free at <http://www.mrc-bsu.cam.ac.uk/bugs/>). The software avoids this tedious formulation as it is designed to construct complex posteriors for the user and to sample them by means of Gibbs techniques (Spiegelhalter *et al.*, 1996).

Slow convergence is a chronic issue in state-space models owing to the high correlation of variables in the time series (Rivot *et al.*, 2004). We followed Kass *et al.* (1998) to ensure convergence. An initial run (5000 iterations of burn-in period plus 10 000 additional iterations) was used to select over-dispersed parameter values. Parameter values for the mean as well as the 5 and 95 percentiles of this initial run initiated three sample chains. The convergence was diagnosed when Gelman and Rubin (Brooks and Gelman, 1998) statistics reached values below 1.2 for the parameters at about 100 000 iterations.

Data

Three sources of data have been used throughout this paper: environmental records as covariates, fisheries information for the observational model and field data of early life stages to validate results.

Sea surface temperature (SST) was derived from data obtained by the Advanced Very High Resolution Radiometer (AVHRR) sensor. The nighttime AVHRR PATHFINDER SST v5 monthly means with $4 \times 4 \text{ km}^2$ pixel resolution were obtained from NASA PO.DAAC website (<http://podaac.jpl.nasa.gov/>). Our

region of interest was extracted from the global image and arithmetic means were calculated based on all pixels within this region. Discharges from the Alcalá del Río dam were provided by *Confederación Hidrográfica del Guadalquivir*. They correspond to the monthly accumulated cubic hectometres that are discharged from the dam each month. Wind data are the monthly accumulated time (in days) that easterlies faster than 30 km h^{-1} have been recorded in the meteorological station of Cádiz. Figure 3 shows the time series of these environmental data for the time period covered by the model.

Annual CPUE data from ICES were transformed into monthly values by assuming the same (ICES) value for all months of that year. This approach was preferred to more sophisticated methods that incorporate monthly changes in CPUE. Exploratory analysis of other (non-ICES) CPUE data with monthly resolution shows signals that are more related to the dynamics of the fishing fleet than to variations of stock size. The relative importance of anchovy and sardine (*Sardina pilchardus*; an alternative, lower price resource) on the total catch of the purse-seine fleet consistently fluctuates from sardine in winter to anchovy in spring and summer, as does the effort expended on both species. However, the low fishing effort expended on anchovy during winter months makes occasional catches result in artifactually high CPUE. ICES acoustic data for the years 1993 and 2004 were selected as reliable estimators of stock size. Although more acoustic data exist for other years, they were not included in the model because they are under review (Anonymous, 2006).

Average monthly egg and larval abundance at the shelf of the Gulf of Cádiz for the years 2002–2004 were obtained from Ruiz *et al.* (2006), where methodological details can be found. Briefly, they

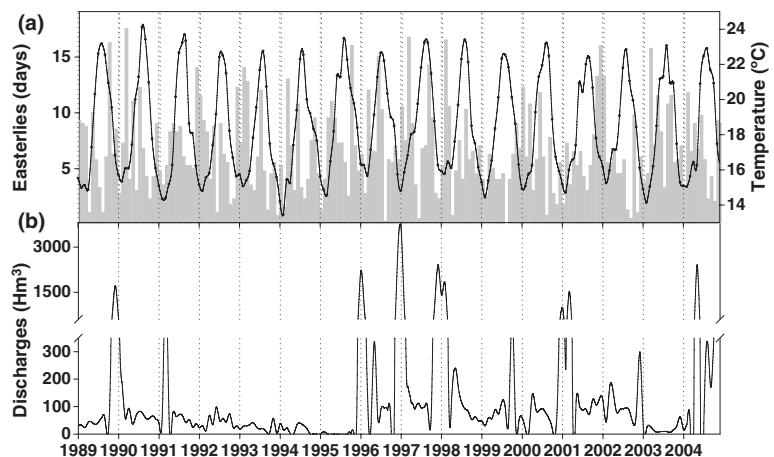
correspond to averages of 26 stations covering the whole north-eastern section of the Gulf with monthly sampling with double-oblique hauls using Bongo nets (40-cm mouth diameter and $200\text{-}\mu\text{m}$ mesh size). Abundance of early stages inside the Guadalquivir River estuary for the years 1997–2004 were taken from Drake *et al.* (2007), where methodological details can be found. Briefly, they correspond to monthly sampling of the last 32 km of the estuary with passive hauls with large nets (2.5-m mouth and 1-mm mesh size) using tidal currents.

RESULTS

Figure 4 shows the *a posteriori* histogram of the model error and parameters, the latter together with their prior probability density functions. Parameter posteriors are less dispersed than priors, evidence of data added to the priors and their effects on model parameters. In addition, posteriors of environmental parameters, such as the thermal (τ) and discharge (ρ) effect, increase their mean value compared to their priors, whereas wind (λ) shows a decrease. This indicates a greater environmental effect than foreseen *a priori* for τ and ρ as well as less of an impact (or a model formulation that does not grasp all the intricacies of the process) for λ . Low values of the mortality parameter (μ) point at the environment and catches as the main factors controlling the population. High mortalities induced by the environment and the fishery reduce μ to values that are negligible for the functioning of the process model.

Posterior probabilities for the different stages of the life cycle show evident seasonal patterns (Fig. 5), with higher larvae concentration usually found during the first half of the year when sea-water heating is manifest (Fig. 3). In addition, larvae showed conspicuous in-

Figure 3. Time series of environmental data-forcing processes in the model. (a) Monthly mean sea surface temperature (line) at the shelf of the Gulf of Cádiz and number of days per month that easterlies faster than 30 km h^{-1} have been recorded at Cádiz meteorological station (bars). (b) Discharge from the Alcalá del Río dam.



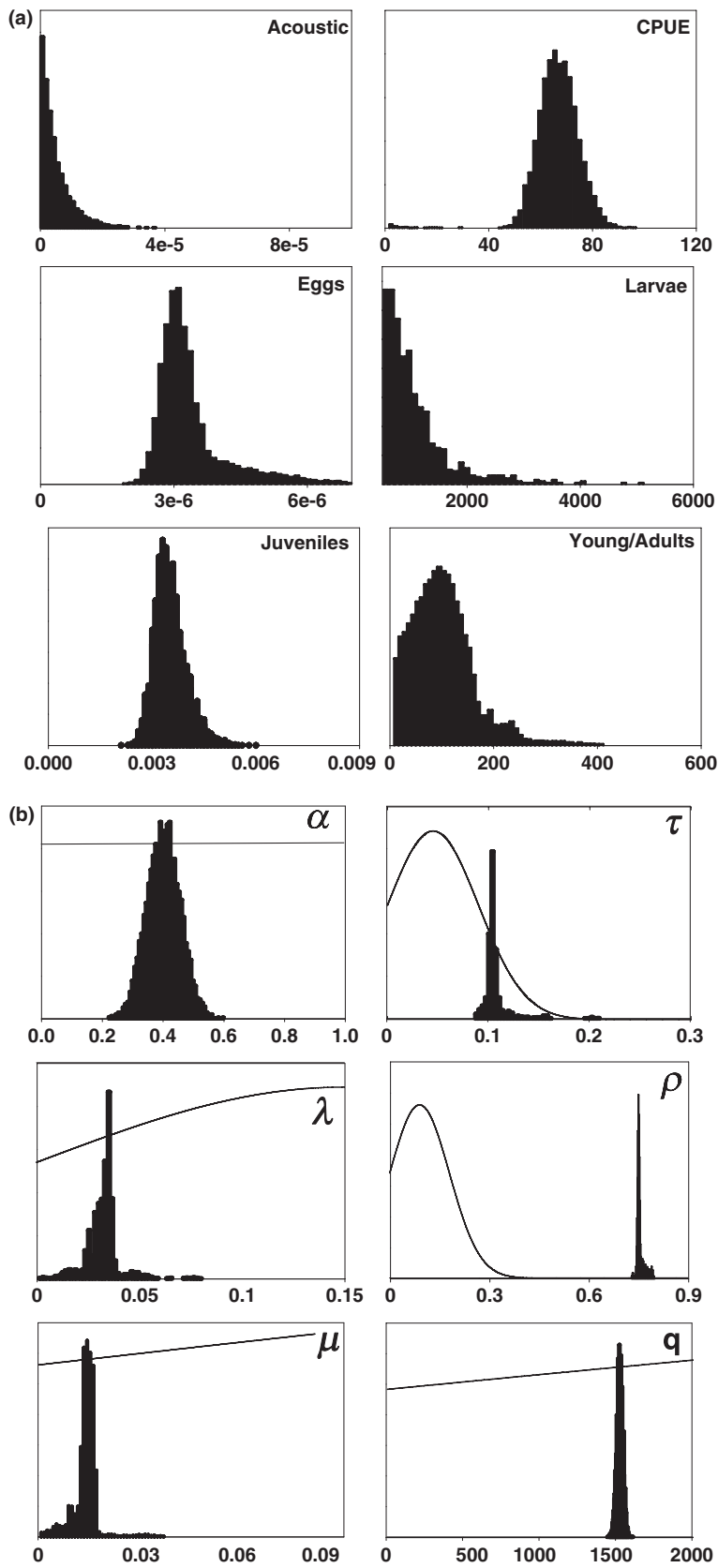
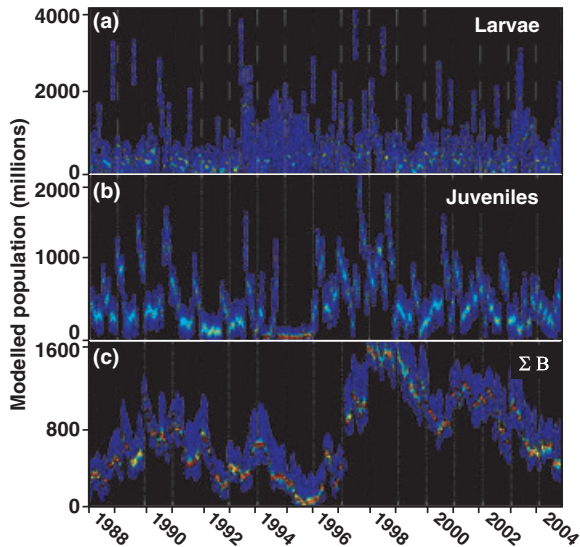


Figure 4. (a) Inverse of error posteriors. (b) Probability density functions (lines) for the priors of the model parameters and *a posteriori* distribution (vertical bars).

Figure 5. Time series of probability for the modelled population abundance of larvae (a), juveniles (b) and stock size ΣB (c).



terannual signals with low values during 1994–1995. During these years, particularly in 1995, the model predicts a severe decline of the juvenile population with a very high level of certainty. The model predicts a sudden end to this decrease of juvenile abundance in 1996, when probability persistently accumulates at population values above the average of the time series. The decline of juveniles in 1995 is preceded by a decline of individuals vulnerable to the fishery (ΣB) which is predicted by the model in the transition between 1994 and 1995. The probability of ΣB then has low population values until 1996, when the model predicts a recovery which, although not as evident as for juveniles in that particular year, is manifest later on. Besides this interannual signal, the probability of ΣB shows a clear seasonal signal with continuous declines after the recruitment occurs early in the year.

Seasonal and interannual fluctuations of ΣB can be better discerned in connection with fishery

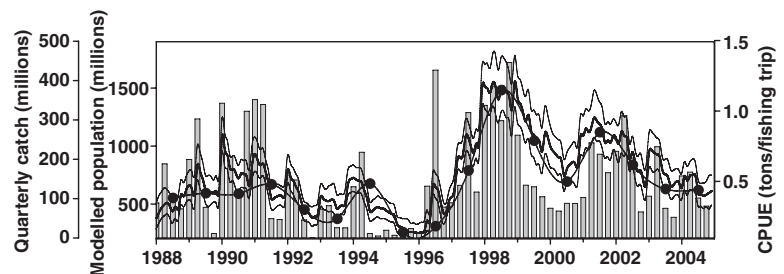
information (Fig. 6). Highs and lows of ΣB and catches evolve consistently. Catch data for 2000 are shaped by a serious societal conflict which dramatically reduced the fishing effort that year. The catch per unit effort (CPUE) is less affected by this feature and its evolution is more coherent with ΣB (which it estimates) than catches for year 2000. The first available CPUE data (until the early 1990s) are, nevertheless, very stable compared with catch and ΣB values. These data are under consideration for review by ICES because of inconsistencies with more recent information obtained from the fishery (Anonymous, 2006).

The consistency of CPUE, catch and ΣB evolution in Fig. 6 partially validates the model outputs. Figure 7 adds to this exercise by comparing predicted egg, larvae and juvenile numbers with *in situ* abundance data when available. Eggs and larvae abundance are derived from Ruiz *et al.* (2006), and juvenile information from Drake *et al.* (2007). The model reproduces the overall pattern of eggs and larvae abundance, although discrepancies also exist in the peak of egg abundance during early 2003. The overall pattern of the modelled juvenile population is also consistent with *in situ* data, except for years such as 1997 when the timing is correct but the magnitude of the modelled peak is greater than observed.

DISCUSSION

Uncertainty is ubiquitous in our knowledge on clupeoid dynamics. Use of fishery, acoustic or egg-production methods to estimate population size is impaired by significant flaws (Brehmer *et al.*, 2006; Stratoudakis *et al.*, 2006). The dynamics itself is highly unstable in connection with environmental and ecological processes, and models do not fully resolve it (Bakun and Broad, 2003). Increased model complexity to resolve the dynamics does not decrease the uncertainty (Hill *et al.*, 2007). More structure implies more assumptions and a decreased capacity to predict beyond calibration data (Anderson, 2005).

Figure 6. Time series of the modelled population of individuals older than 6 months. Thick and thin lines are respectively the mean and the percentiles (5 and 95) of the posterior distribution. Bars and dots are respectively quarterly catch and CPUE from ICES data.



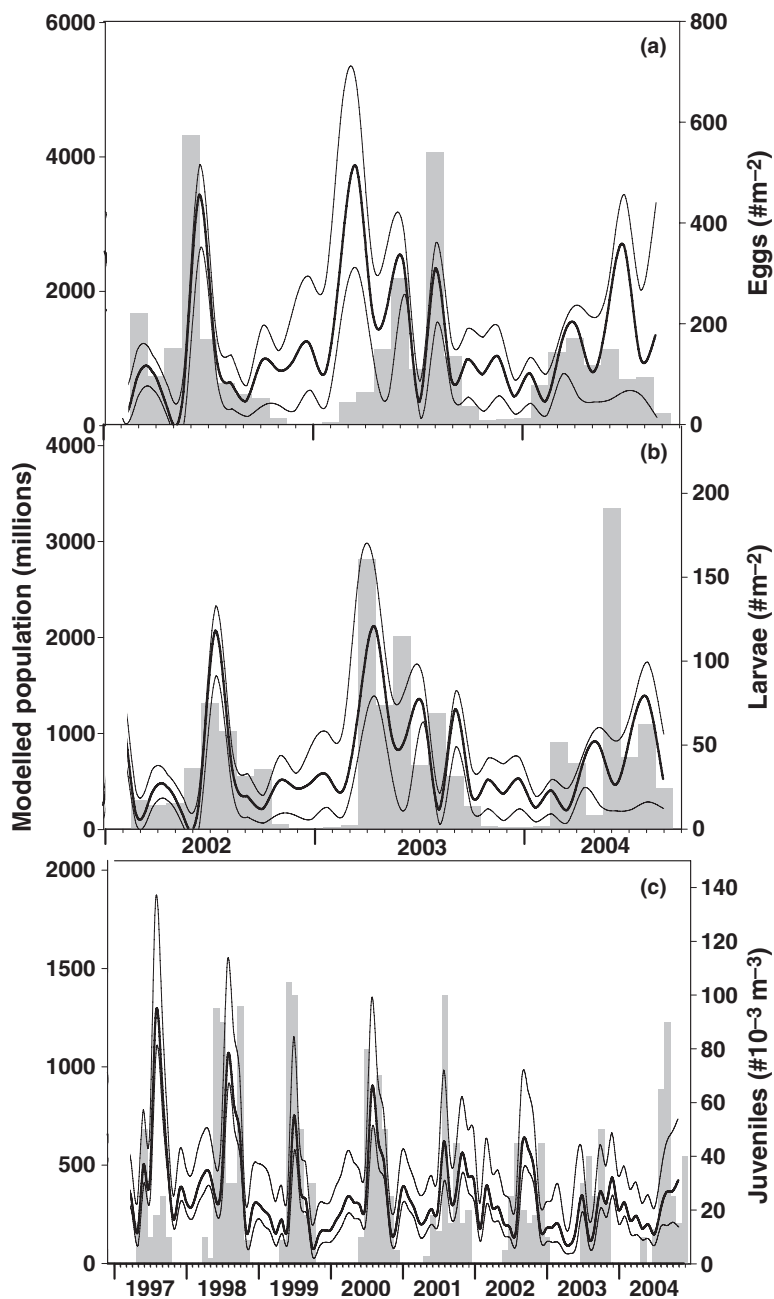


Figure 7. Time series of modelled eggs (a), larvae (b) and juveniles (c) versus abundance recorded at the Gulf of Cádiz shelf (eggs and larvae) and Guadalquivir estuary (juveniles). Thick and thin lines are respectively the mean and the percentiles (5 and 95) for the posterior distribution of variables. Bars are *in situ* abundances.

The model presented above is parsimonious. Its straight connection between the environment and anchovy dynamics implements previous knowledge (Ruiz *et al.*, 2006) with simple equations and few parameters. These elude the intricacies of biogeochemical cycles and trophic interactions that relate physical forcing to anchovy fluctuations. Those intricacies are encapsulated in Equations 1–4. The simplification might generate apparent inconsistencies between model output and validation data such as stock overestimation for the year 2000, egg timing for

the year 2003 or the magnitude of juvenile abundance for the year 1997 (Fig. 7). Considering that observational data are not an exact image of the real world assists in analysing these inconsistencies. For instance, low catches in 2000 do not result from low abundance but from societal issues in the fleet. In this case, the discrepancy between data and model favours model validation, because predictions stay close to CPUE, and the data are not affected.

Including more fishery-independent estimates of stock size to the observational part of the model would

undoubtedly ameliorate its capacity to resolve these discrepancies and, therefore, the response of fish to the environment. Lack of sensitivity to the inclusion of a ‘catchability’ coefficient in Equation 7 indicates that available acoustics estimates of the stock are still too few to significantly impact the overall behaviour of the model. Ibaibarriaga *et al.* (2008) showed that enough fishery-independent information makes Bayesian approaches sensitive to the inclusion of ‘catchability’ coefficients in the observational model. Additional environmental factors could also further improve the fitting of the model to the data. For instance, wind affects both the advection of eggs and larvae (Ruiz *et al.*, 2006) as well as the trophic dynamics of the spawning area (Navarro and Ruiz, 2006). The latter results from Ekman pumping driving coastal upwelling/downwelling, and the subsequent enrichment/impoverishment of nutrients in the surface waters of the shelf. Advection and trophic effects of wind could be distinctly resolved if chlorophyll concentrations derived from the remote sensing of ocean colour were included as an additional covariate. This inclusion would allow simulation of the trophic environment of larvae, a key component of their survival (Blaxter *et al.*, 1982; Painting *et al.*, 1998). However, sea surface colour from SeaWiFS data have only been available since September 1997, and including them in the model implies a non-homogeneous treatment of environmental forcing along the time series. We avoided this inconsistency, which nonetheless seems to decrease the potential of the model for resolving wind effects as the posterior of λ renders the

expected influence of this covariate on stock dynamics lower than *a priori*.

The Bayesian framework consistently transforms into uncertainty components of the dynamics left unresolved by model simplification but still maintains substantial diagnostic power. The main stock collapse in 1995 is explained with a high level of certainty as a failure of recruitment in juveniles in that year in connection with severe decreases of dam discharges (Figs 3 and 5). Juvenile failures were already detected with low uncertainty the year before, when the stock collapse was not yet evident. The concentration of probability at such low values 1 year ahead of the crisis suggests that future developments of the approach could result in some prognostic capacity. This potential was further evaluated by implementing the model with different runs that progressively incorporate the years of the time series (year 2–17). In each run, the distribution of $\sum B/q$ for the last year of the series was predicted without including the observational model for that particular year. Figure 8 shows the $\sum B/q$ predicted with this sequential implementation of the model. At the beginning of the time series, when little information is available to infer parameter posteriors, the predictions significantly differ from data and uncertainty is large. However, uncertainty decreases as the model ‘learns’ from the data and the evolution of the predicted $\sum B/q$ is coherent with the tendencies of CPUE observed later. This coherence must, nevertheless, be analysed with caution as the process model includes observed catch and environmental data in the prediction. However, the coherence between the predicted $\sum B/q$ and the later observed CPUE supports

Figure 8. $\sum B/q$ predicted (lines) versus CPUE observed (bars) for the sequential implementation of the model along the time series. Thick and thin lines are respectively the mean and the percentiles (5 and 95).

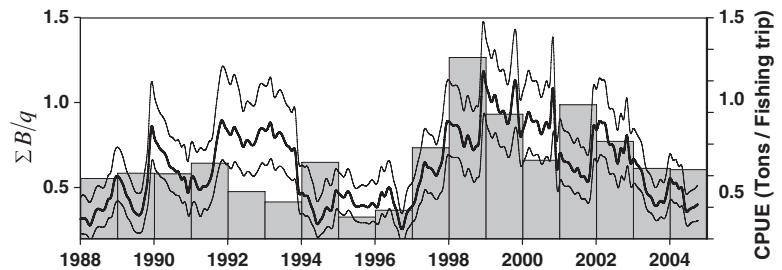
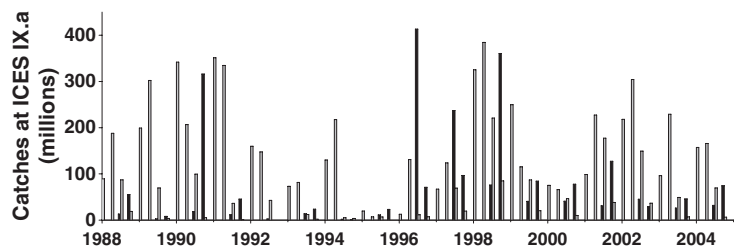


Figure 9. ICES quarterly catches of anchovies of year group 0+ and 1+ (black and grey bars, respectively).



the use of this approach to analyse the outcome of potential future scenarios (meteorological regime and catches) on the evolution of the stock size.

Moreover, the model predicts the breakaway from the crisis with three successive years (1996–1998) when juvenile probability is concentrated at values above standard levels (Fig. 5). Age composition of catches depicts a contribution of the 0+ year group that is also above the average for that period (Fig. 9), thus indicating the singular abundance of small fish at that time. It is noteworthy that Equations 1–7 have no contact with the age or size structure of the catch. Hence, the ability of the model to reproduce this feature is process- and not data-driven. Similarly, Equations 6 and 7 do not assimilate data of Fig. 7 and the capacity of the model to reproduce the pattern of egg, larvae or juvenile abundance is process-driven.

This model demands few process parameters in comparison with other modelling approaches. Six parameters (α , μ , τ , λ , ρ and q) plus their errors implement the population dynamics as well as its connection with the environment and observational data. In comparison, Fasham *et al.* (1990) and ERSEM (Vichi *et al.*, 2007) models demand respectively 45 and more than 130 parameters. For anchovy in this region, this simple structure is able to reproduce the major dynamical features detected by the information available on fishery and life stages. Ruiz *et al.* (2007) point out that this dynamics is a case of BOT-TOP control. Under this type of control the fishing pressure restrains the population from the top and prevents adults from surviving beyond 1 year. Without sustenance of adults, the population relies totally on recruits to persist. Owing to the vulnerability of early stages to ocean processes, the stock is then totally controlled by environmental fluctuations. This is a neat case of fish dynamics forced by the environment and not necessarily easy to extrapolate to other anchovy populations. However, at least for the Gulf of Cádiz, a simple Bayesian model that represents our lack of knowledge as uncertainty characterizes anchovy dynamics well beyond the trivial fact that fish populations fluctuate.

ACKNOWLEDGEMENTS

This work was funded by the *Consejería de Agricultura y Pesca de Andalucía* as well as by projects P06-RNM-02393 from *Junta de Andalucía* and SESAME (FP6-036949). Meteorological data were provided by the *Agencia Estatal de Meteorología*. The manuscript has been greatly improved during the review process thanks to the anonymous contribution of referees.

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