Bayesian state-space modelling of the De Lury depletion model: strengths and limitations of the method, and application to the Moroccan octopus fishery

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The strengths and limitations of a Bayesian state-space modelling framework are investigated for a De Lury depletion model that accommodates two recruitment pulses per year. The framework was applied to the Moroccan fishery for common octopus (*Octopus vulgaris*) between 1982 and 2002. To allow identifiability, natural mortality (M) and the recruitment rhythm were fixed, and the variance of both process and observation errors were assumed to be equal. A simulation–estimation (SE) approach was derived to test the performance of the method. If the data showed responses to harvest, the estimates of the most important figures, i.e. the initial abundance and the second recruitment pulse, were accurate, with relatively small bias. Results confirm that greater depletion yields smaller bias and uncertainty and that inferences are sensitive to the mis-specification of M. The 21 depletion series in the Moroccan dataset were jointly treated in a hierarchical model including random walk to capture the systematic fluctuations in estimates of catchability and initial abundance. The model provides estimates of the annual recruitment and monthly octopus population size. The recruitment estimates could be used to investigate the link between recruitment variability and the coastal North African upwelling regime to improve understanding of the dynamics and management of octopus stocks.

Keywords: Bayesian, De Lury depletion model, hierarchical model, MCMC, octopus, recruitment, state-space modelling.

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Introduction

Cephalopods are of increasing commercial fisheries importance worldwide (Caddy and Rodhouse, 1998; Payne *et al.*, 2006). Most commercially important cephalopod species have a short life cycle, grow rapidly, and are semelparous. Catches show large year-on-year fluctuations driven by the influence of environmental conditions on recruitment (Agnew *et al.*, 2000; Faure *et al.*, 2000; Otero *et al.*, 2008; Pierce *et al.*, 2008). Owing to poor knowledge of their biology and ecology and to their short lifespan, the assessment of cephalopod stocks requires specialized methodology. As age determination is difficult, biomass surplus production models are often used for stock assessments (FAO, 2006). However, providing management advice based on the results from annual surplus production models may not be the most suitable approach for managing cephalopod fisheries. Indeed, few generations overlap, stocks respond at fine time-scales to fluctuations in the environment and fishing pressure, and within-season advice is often needed (Pierce and Guerra, 1994; Payne *et al.*, 2006).

Several authors have suggested that stock assessment of such short-lived species should combine long- or medium-term assessment methods (e.g. annual biomass surplus production models) with short-term in-season assessments based on models running on shorter (typically monthly or weekly) time-steps (Pierce and Guerra, 1994; Agnew *et al.*, 1998; Roa-Ureta and Arkhipkin, 2007). Depletion models (Leslie and Davis, 1939; De Lury, 1947) are good candidates for in-season monitoring and management of cephalopod fisheries. Intense rates of exploitation generally induce sharp depletions in abundance after the main recruitment within a year. The depletion model is designed to capture such within-season dynamics and can be used to track in real time the depletions in abundance under fishing pressure (Pierce and Guerra, 1994; Agnew *et al.*, 1998; Young *et al.*, 2004), allowing in-season adaptations of management measures. Forecasts under alternative scenarios of fishing effort can also be derived, so allowing evaluation of whether the initial potential of the stock was under- or over-appraised, and adjustment of effort and catches for the end of the fishing season. Depletion models have been applied successfully in the assessment of the squid stock of the Falkland Islands within a frequentist statistical approach (Beddington *et al.*, 1990; Rosenberg *et al.*, 1990; Agnew *et al.*, 1998; Roa-Ureta and Arkhipkin, 2007) and a Bayesian approach (McAllister *et al.*, 2004). Royer *et al.* (2002) used a depletion model to study squid recruitment in the English Channel. Depletion models have also been used to describe the dynamics

of other exploited species, such as Cuban shelf spiny lobster (González-Yáñez *et al.*, 2006).

Although process noise and observation errors are not uncommon in fisheries models, the depletion model has never been considered in a state-space modelling (SSM) framework accounting for both sources of errors. This work investigates the strengths and limitations of a Bayesian SSM (BSSM) framework for the De Lury depletion model, with an application to the Moroccan fisheries of common octopus (*Octopus vulgaris*) between 1982 and 2002. We offer three substantial new contributions. First, as far as we can ascertain, the work provides the first BSSM approach of the De Lury depletion model including both process and observation errors and an estimation of a secondary recruitment pulse. Second, extensive evaluation of the sensitivity of a Bayesian version of this model to alternative model forms and data configurations is provided. Third, the hierarchical Bayesian approach of McAllister *et al.* (2004) was extended by introducing a random-walk formulation to capture the systematic fluctuations of the time-series of initial abundance and catchability.

A vast continental shelf combined with the large and permanent Canarian upwelling system makes NW African waters one of the world's richest fishing grounds (Balguerías *et al.*, 2000). Octopus fisheries are of great social and economic importance in the region, especially in Morocco (Faraj and Bez, 2007). Moroccan catches attributed to *O. vulgaris* have shown marked fluctuations, with maxima in 1991 and 2000 (around 110 000 t) and minima in 1997 and 2003 (50 000 and 25 000 t, respectively; FAO, 2006). Stock assessments, mostly based on surplus production models, reveal that octopus stocks in the region have been overexploited since the end of the 1980s (FAO, 2006). The depletion model has recently been advocated as a method of choice to be implemented in the region (Faraj *et al.*, 2006), because it allows conducting of in-season stock assessment and management. A depletion model was developed for the Moroccan case study. Octopus along the Moroccan coast show two recruitment pulses per year (Balguerías *et al.*, 2002; Faraj and Bez, 2007). The main recruitment is in autumn and catch rates peak around November. A secondary recruitment pulse appears during spring. Hence, the depletion model was extended to include the spring recruitment (Royer *et al.*, 2002; González-Yáñes *et al.*, 2006).

The depletion model was developed within a Bayesian framework because that provides a flexible rationale for stochastic statistical modelling, inferences, and predictions (Ellison, 2004; Clark, 2005). Since the 1990s, the Bayesian framework has been widely applied in fisheries sciences (Walters and Ludwig, 1994; Punt and Hilborn, 1997; McAllister and Kirkwood, 1998; Harwood and Stokes, 2003). It allows the integration of different types of information (Hilborn and Lierman, 1998) and multiple sources of uncertainty in data and models. Diagnostics and predictions are derived using probabilistic rationale, and results are easily embedded within a formal decision analysis. In particular, BSSM coupled with sequential Monte Carlo methods such as Markov Chain Monte Carlo (MCMC) simulations have proved able to handle discrete-time dynamic models with process error stemming from uncertainty in the dynamics of the system and measurement and sampling errors in the data (Meyer and Millar, 1999; Millar and Meyer, 2000; Buckland *et al.*, 2004; Rivot *et al.*, 2004; Thomas *et al.*, 2005; Swain *et al.*, 2009).

A simulation–estimation (SE) analysis was conducted to assess the strengths and limitations of the approach. Even if the

methodology is technically well established, deriving Bayesian inferences on a SSM is a non-trivial task. Fitting models to simulated data helps to determine the performance of the method, because the true values of the parameters used in the simulation are known. SE approaches have been widely used in the frequentist framework (for recent examples, see Punt, 2003; Magnusson and Hilborn, 2007; Trenkel, 2008). The analyses are less immediate and more laborious in the Bayesian framework, and examples are rarer (see Hammond and Trenkel, 2005; Tang and Heron, 2008; Zhang *et al.*, 2009, for recent examples). In the current work, special attention is devoted to the SE approach designed to assess the performance of the estimation method under different data and model configurations.

The framework was applied to analyse catches and catch per unit effort (cpue) data from the Moroccan octopus fishery between 1982 and 2003. The 21 depletion series were jointly treated in a hierarchical model. Hierarchical Bayesian models have been advocated as appropriate methods to analyse jointly a population of similar datasets that share common characteristics (Rivot and Prévost, 2002; Gelman *et al.*, 2004; McAllister *et al.*, 2004; Rivot *et al.*, 2008). They offer a probabilistic structure to model the cross-population variability in parameters that underlies different datasets and to derive posterior predictive distributions for the parameters of a yet unsampled dataset. McAllister *et al.* (2004) applied Bayesian hierarchical modelling (BHM) to a set of historical depletion series for Falkland Islands squid. They show how hierarchical modelling probabilistically shares information among the different depletion series and improves the estimation of key parameters. The hierarchical structure they proposed was extended by introducing random walk (RW) to capture autocorrelated fluctuations in the time-series of initial abundance and catchability. Indeed, the values of N_1 are likely to show autocorrelated fluctuations because of the population dynamics and environmental influences. Fishing efficiency is also likely to show fluctuations caused by gradual changes in behaviour and technological improvements to the fishing fleet.

Material and methods
Data

The depletion model was used to mimic the decrease in abundance (in numbers) of octopus in Morocco for 21 depletion series between 1982 and 2003. For each series, the model was built on a monthly time-step. In Moroccan waters, the maximum abundance of octopus is observed in November, the opening of the fishery (Figure 1). Overall, there were 21 depletion series beginning in November 1982 (Figure 2). The data used in this work were collected by the Moroccan Institute for Fisheries Research (INRH) and the Moroccan Fisheries Department (Faraj *et al.*, 2006), and the methods used to calculate monthly catches and cpue for the period 1982–2003 are presented below.

Total annual catches in Moroccan waters (Moroccan catches for the artisanal, coastal, and industrial fleets, and catches of the foreign industrial fleet) were available for the years 1982–2003. First, total annual catches were disaggregated to a monthly time-step, based on a survey of the industrial Moroccan fleet, because a survey of the other fleets did not provide the same level of information. Second, monthly catches by weight were converted to numbers via an average weight-at-month relationship. This relationship was established from samples taken from artisanal and coastal landings between 2001 and 2005.
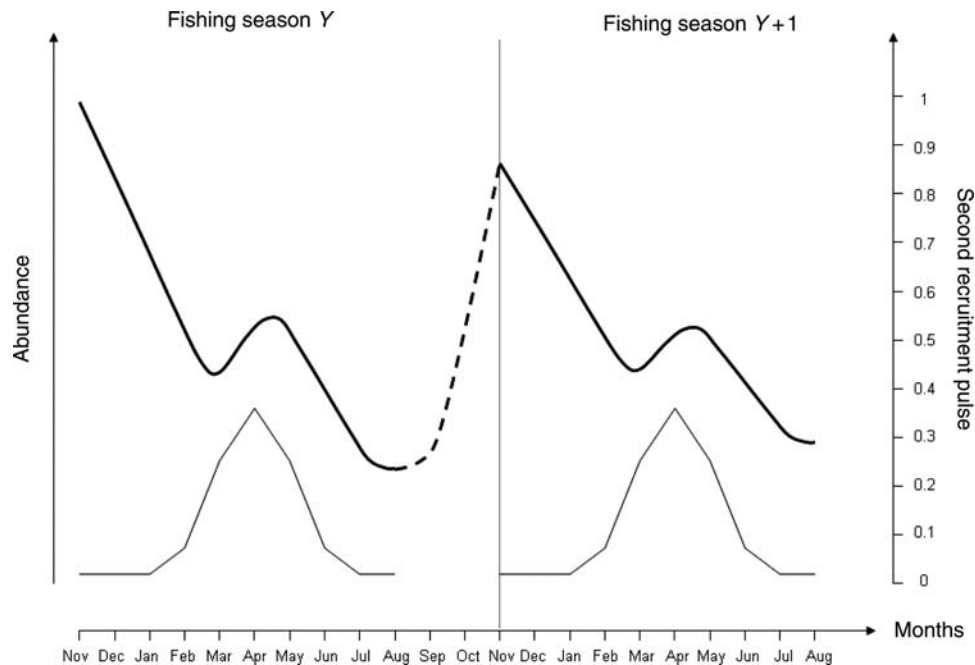
Figure 1. Schematic diagram of the shape of the abundance trajectory (arbitrary units) of octopus in Moroccan waters. The thick line depicts the typical shape (arbitrary units) of the abundance observed from abundance indices (solid line) and unobserved (dashed line). The main recruitment pulse is just before the opening of the fishing season, typically in November. The thin line depicts the proportion of the secondary recruitment R that occurs each month; it takes place between February and June, with a peak in April (values are given in text).

The cpue series of the industrial Moroccan fleet were used. The cpue was calculated monthly by dividing the catches (in numbers as defined above) by the duration of the trip (in days at sea). From the 1982–2003 time-series of catches and cpue (monthly time-step), 21 depletion series were selected according to the typical shape of the abundance during one fishing season (Figure 1) and to a decision rule: for each season, the start of each depletion series (associated with the highest cpue value) was defined as the opening of the fishery, and the end of the depletion series was considered as the inflection point in the series of cpue just before the opening of the fishery season the following year (Figure 1). Roughly speaking, all depletion series start in November, but the duration of the series is not constant over the time-series (Table 1).

BSSM of the depletion model

Dynamic equation

Depletion models are based on a discrete-time sequential equation that mimics the decrease in the abundance (in numbers) of a closed population in response to removals (Rosenberg et al., 1990; Gonzalez Cano and Restrepo, 2001). Rosenberg et al. (1990) proposed a model that assumes that the abundance at time-step $t + 1$ depends on the abundance at time t, the cumulative catches c_t between t and $t + 1$, and natural mortality, M. The latter rate is assumed constant over time. The process is initialized by the initial abundance, N_1. Following Royer et al. (2002) or González-Yáñes et al. (2006), a secondary recruitment pulse for Moroccan octopus was accounted for by modifying the depletion model to incorporate a secondary recruitment, denoted R, within the fishing season [Equation (1)] with a certain rhythm. The recruitment rhythm is denoted $(\lambda_1, \ldots, \lambda_n)$, with λ_t defined as the proportion of R that takes place in month t (and the values

of λ_t sum to 1). The recruitment rhythm was considered known to ensure that all parameters can be estimated (Royer et al., 2002). According to Pope's approximation (Pope, 1972), we considered the cumulative catches (c_t) and the recruitment $\lambda_t R$ as punctual events occurring exactly in the middle of the period $[t, t + 1]$. Process errors were assumed to be independent and identically distributed (iid) multiplicative lognormal (Halley and Inchausti, 2002) with variance σ_p^2:

$$N_{t+1} = (N_t e^{-M} - c_t e^{-M/2} + \lambda_t R e^{-M/2}) e^{\varepsilon_t}$$

$$\text{with} \quad \varepsilon_t \overset{\text{iid}}{\sim} N(0, \sigma_p^2) \quad \text{for } t = 1, \ldots, n - 1, \tag{1}$$

where N_1 is the initial abundance.

The initial population size N_1, interpreted as the intensity of the main recruitment event, is in November (the opening of the fishery). Therefore, in our model, $t = 1$ is in November of calendar year a. The secondary recruitment contributes to the fishery from spring to the end of summer (Figure 1) of calendar year $a + 1$.

Observation equation

Estimation procedures rely on the fact that removing individuals from a population has a noticeable effect on some observable abundance index. A linear relationship is classically assumed between observed abundance indices i_t and unobserved abundance N_t, with a scaling factor q considered as constant over time. As i_t is a cpue and because catches are assigned to the middle of the time-step, the abundance index is assumed to be proportional to the mean abundance between time-step t and $t + 1$. As for process errors, observation errors were assumed to be iid multiplicative
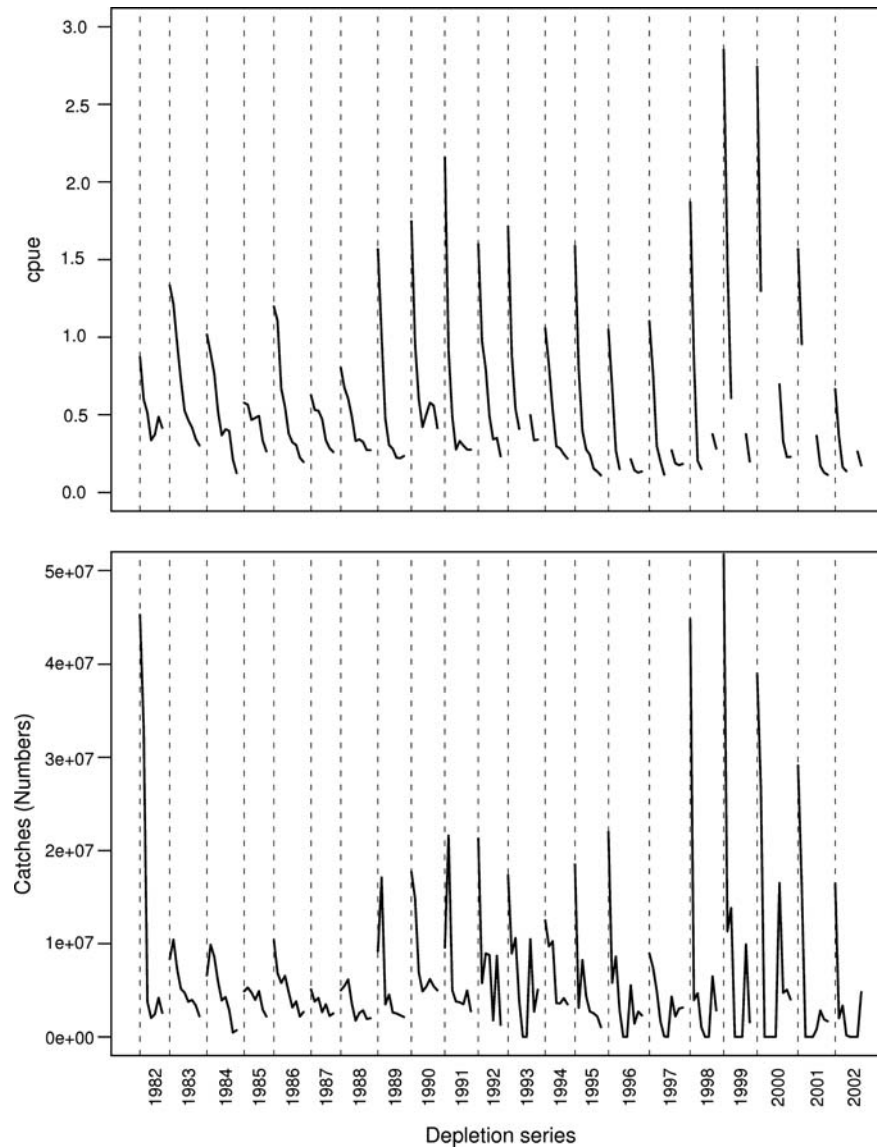
Figure 2. Total catches (in numbers) and abundance indices (cpue of the industrial fleet; thousands per day at sea) for the Moroccan fishery of octopus between 1982 and 2002. Catches and abundance indices are plotted on monthly time-steps for the 21 depletion series.

lognormal with variance σ_o^2:

$$i_t = q\left(\frac{N_t + N_{t+1}}{2}\right)e^{\omega_t}$$

(2)

with $\quad \omega_t \stackrel{\text{iid}}{\sim} N(0, \sigma_o^2) \quad$ for $t = 1, \ldots, n-1$.

The classical estimation approach relies on rewriting Equation (1) for each time-step t (with $R = 0$ and no process error) as a function of the initial population size N_1, and cumulative catches between $t = 1$ and t. Then, substituting N_t by i_t/q, and assuming an observation error on the abundance indices, the parameters N_1 and q can be estimated by regressing abundance indices against cumulative catches [possibly in log-scale; Equation (3)]. The estimates of q and N_1 are highly correlated because those parameters appear as a product in Equation (3). The performance of the estimation depends on the depletion intensity: the stronger

the slope of the regression, the better the quality of the estimates (Agnew *et al.*, 1998; McAllister *et al.*, 2004; Magnusson and Hilborn, 2007):

$$i_t = qN_1e^{-(t-1)M} - q\sum_{j=1}^{j=t-1} c_j e^{-(t-j-0.5)M}.$$

(3)

Including recruitment R and considering the model in an SSM framework with both process errors [Equation (1)] and observation errors [Equation (2)] markedly complicates the estimation. Process errors in the dynamic propagate across time, and the abundance indices i_t can no longer be expressed as a simple function of N_1 and cumulative catches. Applying a Bayesian Monte Carlo approach for parameter estimation allows us to overcome this difficulty and to approximate the posterior distributions of all unknown variables in the model.

Table 1. Dates of the start and the end of each of the 21 selected depletion series (start years 1982–2002).

Depletion series	Start	End
1	November 1982	April 1983
2	October 1983	June 1984
3	October 1984	June 1985
4	September 1985	March 1986
5	October 1986	June 1987
6	December 1987	June 1988
7	October 1988	June 1989
8	November 1989	June 1990
9	November 1990	June 1991
10	November 1991	June 1992
11	October 1992	April 1993
12	November 1993	July 1994
13	November 1994	May 1995
14	November 1995	June 1996
15	November 1996	August 1997
16	November 1997	August 1998
17	November 1998	June 1999
18	November 1999	June 2000
19	November 2000	August 2001
20	December 2001	August 2002
21	December 2002	July 2003

Table 2. Prior distributions for the four unknown parameters of the reference scenario of the SE approach (S1).

Parameter	Distribution	Parameter
N_1	$\sim$Lognormal	Mode $= 10^8$, $CV = 2$
R	$R = \alpha_R N_1$	$\alpha_R \sim$ uniform (0,1)
q	$\sim$Lognormal	Mode $= 10^{-7}$, $CV = 2$
σ^2	$\log(\sigma^2) \sim$ uniform	$CV_{min} = 0.01$, $CV_{max} = 10$;
	$(\log(\sigma^2_{min}), \log(\sigma^2_{max}))$	$\sigma^2 = \log(CV^2 + 1)$

Lognormal priors were specified in terms of the mode and the CV so as to better monitor their shape. σ^2 refers to the variance of the process and observation errors (supposed equal). The prior on the secondary recruitment specifies that R is *a priori* lower than the initial abundance N_1.

Fixed parameters

To ensure that all parameters can be estimated, further hypotheses were formulated and several parameters were fixed according to the Moroccan case study. Process and observation error variances were set to be equal: $\sigma^2_o = \sigma^2_p = \sigma^2$. The magnitude of process and observation errors can seldom be specified *a priori*. In the absence of any information on σ^2_o and σ^2_p, identifiability of the two variances is not guaranteed in SSM, and fixing the ratio of variances ψ was needed to reduce the number of unknown parameters. Inferences in SSM are seldom sensitive to the value of ψ, unless it strongly favours observation or process error (Kimura *et al.*, 1996; Schnute and Kronlund, 2002; Punt, 2003). Therefore, in the absence of any particular information on the relative magnitude of process vs. observation error when analysing real datasets, $\psi = 1$ was used as a default choice.

The rate of natural mortality, M, was fixed at 0.1 month^{-1} and considered to be constant. This corresponds to a survival rate of $<$20% after 1.5 years for this short lifespan species.

The rhythm with which secondary recruitment occurs in the fishery was considered known. It was defined from previous studies (Balguerías *et al.*, 2002) and knowledge from local experts (AF, pers. obs.). The secondary recruitment pulse was considered to take place between February and June, with a peak in April. The following values were considered: $\lambda = 0.01$, 0.01, 0.01, 0.06, 0.24, 0.35, 0.24, 0.06, 0.01, and 0.01 (Figure 1).

Priors

The priors set on the parameters N_1, R, q and the variance σ^2 in the baseline version of the model are defined in Table 2. Priors on N_1 and R were defined as rather weak lognormal. For each depletion series, R was defined *a priori* as a fraction α_R of N_1, with α_R (one for each depletion series) being drawn in a uniform (0,1) prior distribution. This introduced the reasonable *a priori* constraint that the secondary recruitment R is less than the primary recruitment N_1. The logarithm of the process error variance was given a

uniform prior with large bounds to mimic a non-informative prior in the sense of Jeffrey (Millar, 2002; Gelman *et al.*, 2004).

SE approach
Flow chart of the approach
The performance of the estimation method was evaluated using simulated data. The flow chart of the SE approach has three steps.

Step 1: Simulation. Simulate abundance, catches, and abundance index trajectories according to an operating model with known parameters and randomness included in both process and observations. Each scenario first consisted of fixing a set of parameters (M, q, R, N_1, $\{\lambda_t\}_{t=1,...,n}$, σ^2, and monthly harvest rates $\{h_t\}_{t=1,...,n}$) which were used to simulate trajectories of abundance $\{N_t\}_{t=1,...,n}$, catches $\{c_t\}_{t=1,...,n}$, and abundance indices $\{i_t\}_{t=1,...,n}$ following Equations (1) and (2). To remain consistent with Pope's approximation in Equation (1), catches were simulated as $c_t = h_t N_t e^{-M/2}$. The trajectories were simulated over $n =$ 10 time-steps, the maximum length (in months) of a fishing season in Morocco. To evaluate the average performance of the estimation method, 50 repetitions of the SE procedure were conducted for each scenario (see below). Preliminary analyses showed that 50 trials were sufficient to obtain a stabilized evaluation of the performance of the method.

Step 2: Bayesian estimation. Consider the simulated catches and abundance index trajectories as data and use the Bayesian framework to estimate the abundance trajectory and the underlying parameters. For each simulated dataset $\{i_t, c_t\}_{t=1,...,n}$, a Bayesian estimation of unknown variables (q, σ^2, R, $\{N_t\}_{t=1,...,n}$) was performed. M and $\{\lambda_t\}_{t=1,...,n}$ were considered known in the estimation. Note that for almost all scenarios, the model used for the estimation was the same as the operating model used for simulating the data. This ensured that any differences between simulated and estimated quantities were attributable to the performance of the estimation method and not to model mis-specification. A model error, i.e. a difference between the operating model and the simulated model, was introduced only in a few scenarios to assess the sensitivity of the method to mis-specification of M and λ and to the hypothesis made on the error structure.

Step 3: Quantification of the quality of the estimations. The performance of the estimation method was evaluated with respect to how well the marginal posterior distribution of each parameter or unknown state variable estimated the true or simulated value. The evaluation uses three complementary criteria. First, the mean relative error (MRE) was calculated to quantify the bias of the Bayesian estimation. For each parameter θ and each simulation s ($s = 1, ..., 50$), the relative error RE(θ_s) was calculated following Equation (4a), with $E(\theta|data_s)$ the expected posterior mean of

Table 3. Characteristics of the 16 scenarios tested in the SE approach.

Scenario	Simulation					Estimation				
						Prior on N_1		M	Missing data	Error structure
	Depletion at 3 months	CV	λ	M	Fishery closure	CV	Mode			
S1	High	0.1	Base	0.1	No	2	10^8	0.1	No	SSM
S2	**Low**	0.1	Base	0.1	No	2	10^8	0.1	No	SSM
S3	High	0.1	Base	**0.2**	No	2	10^8	**0.2**	No	SSM
S4	High	**0.2**	Base	0.1	No	2	10^8	0.1	No	SSM
S5	High	**0.3**	Base	0.1	No	2	10^8	0.1	No	SSM
S6	High	0.1	Base	0.1	No	**5**	10^8	0.1	No	SSM
S7	High	0.1	Base	0.1	No	2	**10^7**	0.1	No	SSM
S8	High	0.1	Base	0.1	No	2	**10^9**	0.1	No	SSM
S9	High	0.1	Base	**0.2**	No	2	10^8	0.1	No	SSM
S10	High	0.1	Base	0.1	No	2	10^8	**0.2**	No	SSM
S11	High	0.1	**Earlier**	0.1	No	2	10^8	0.1	No	SSM
S12	High	0.1	**Later**	0.1	No	2	10^8	0.1	No	SSM
S13	High	0.1	Base	0.1	**t = 4, 5, 6**	2	10^8	0.1	**t = 4, 5, 6**	SSM
S14	High	0.1	Base	0.1	**t = 3, 4, 5, 6**	2	10^8	0.1	**t = 3, 4, 5, 6**	SSM
S15	High	0.1	Base	0.1	No	2	10^8	0.1	No	**OBS**
S16	High	0.1	Base	0.1	No	2	10^8	0.1	No	**PROC**

Cells with emboldened typeface indicate characteristics that changed in reference to scenario S1 (either in the simulation or the estimation phase). All scenarios used $q = 10^{-7}$ to simulate abundance indices, and $\alpha_R = 1/3$ to simulate R. CV is the coefficient of variation for both observation and process errors. We used the relationship $\sigma^2 = \log(CV^2 + 1)$ that works for lognormal distributions. In S1, the exploitation rate is fixed at 0.3 month^{-1}, and M = 0.1 month^{-1}, generating a depletion rate of 50% after 3 months and 80% after 10 months. In S2, the exploitation rate is fixed at 0.13 month^{-1}, generating a depletion rate of 30% after 3 months and 60% after 10 months. In all scenarios except S11 and S12, the parameter λ used for the recruitment rhythm is the one given in the Methods section. Data for S11 and S12 were simulated by using a series $\{\lambda_t\}_{t=1,\ldots,n}$ that is 1-month lagged backward and forward, respectively, from the reference rhythm. For estimation purposes, all priors are defined in Table 2, and all scenarios are fitted with the reference recruitment rhythm λ. S15 is fitted under the hypothesis of there being observation error only, and S16 of there being process stochasticity only.

θ given the data of the simulation s. For each scenario, MRE(θ) is interpreted as the relative bias [Equation (4b)]:

$$\text{RE}(\theta_s) = \frac{E(\theta|\text{data}_s) - \theta_{\text{true}}}{\theta_{\text{true}}} \quad \text{for } s = 1, \ldots, 50, \quad (4a)$$

$$\text{MRE}(\theta) = \frac{1}{50} \sum_{s=1}^{50} \text{RE}(\theta_s). \quad (4b)$$

Second, the mean standard deviation (MSD) was calculated [Equations (5a) and (5b)], to measure the precision of the Bayesian estimation:

$$\text{SD}(\theta_s) = \sqrt{\text{Var}(\theta|\text{data}_s)} \quad \text{for } s = 1, \ldots, 50, \quad (5a)$$

$$\text{MSD}(\theta) = \frac{1}{50} \sum_{s=1}^{50} \text{SD}(\theta_s). \quad (5b)$$

Third, for each scenario, we computed the standard deviation of the 50 posterior medians, denoted SDE, providing a measure of the variability of the estimates in the 50 simulations.

The 16 scenarios

In all, 16 contrasting scenarios (summarized in Table 3) were defined by adopting different specifications of parameters M, $\{\lambda_t\}_{t=1,\ldots,n}$, $\{h_t\}_{t=1,\ldots,n}$, and σ^2 (simulation and estimation steps), and different specification of priors for N_1, R, q, and σ^2 (estimation step). For illustration, the 50 trajectories of abundance $\{N_t\}_{t=1,\ldots,n}$, catches $\{c_t\}_{t=1,\ldots,n}$, and abundance indices $\{h_t\}_{t=1,\ldots,n}$ obtained for three contrasting scenarios are plotted on Figure 3. The value of hierarchical modelling has been demonstrated previously

(Rivot and Prévost, 2002; Gelman *et al.*, 2004; McAllister *et al.*, 2004), so the performance of hierarchical modelling was not explored through the SE approach. The value of the SSM approach in analysing sequential fishery data has also been demonstrated in other applications (see Punt, 2003, for a recent application to surplus production models). Therefore, SSM was our favoured default approach and the SE study mainly focused on contrasting scenarios designed to investigate five key issues:

(i) Are the estimates sensitive to the quantity of information contained in the dataset? We focused on two particular issues, the strength of depletion in the abundance index trajectory, and the level of process and observation noise.

(ii) Are the inferences sensitive to the prior on N_1?

(iii) Are the inferences sensitive to mis-specification of M and of the secondary recruitment rhythm?

(iv) Are the inferences sensitive to the presence of missing data in the abundance index time-series as a result of fishing moratoria?

(v) Are the inferences sensitive to the error structure in the model? We compared the SSM estimation method with the observation error method (OBS) that ignores the process errors in the statistical procedure, and with the process error method (PROC) that ignores the observation errors.

Reference configuration (S1). All scenarios are variants of the reference configuration S1 that was built from expertise and considered to represent an archetype for the analysis of the Moroccan octopus fishery data. To simulate configuration S1, the exploitation rate was set to be high ($h = 0.3$ month^{-1}), leading to strong
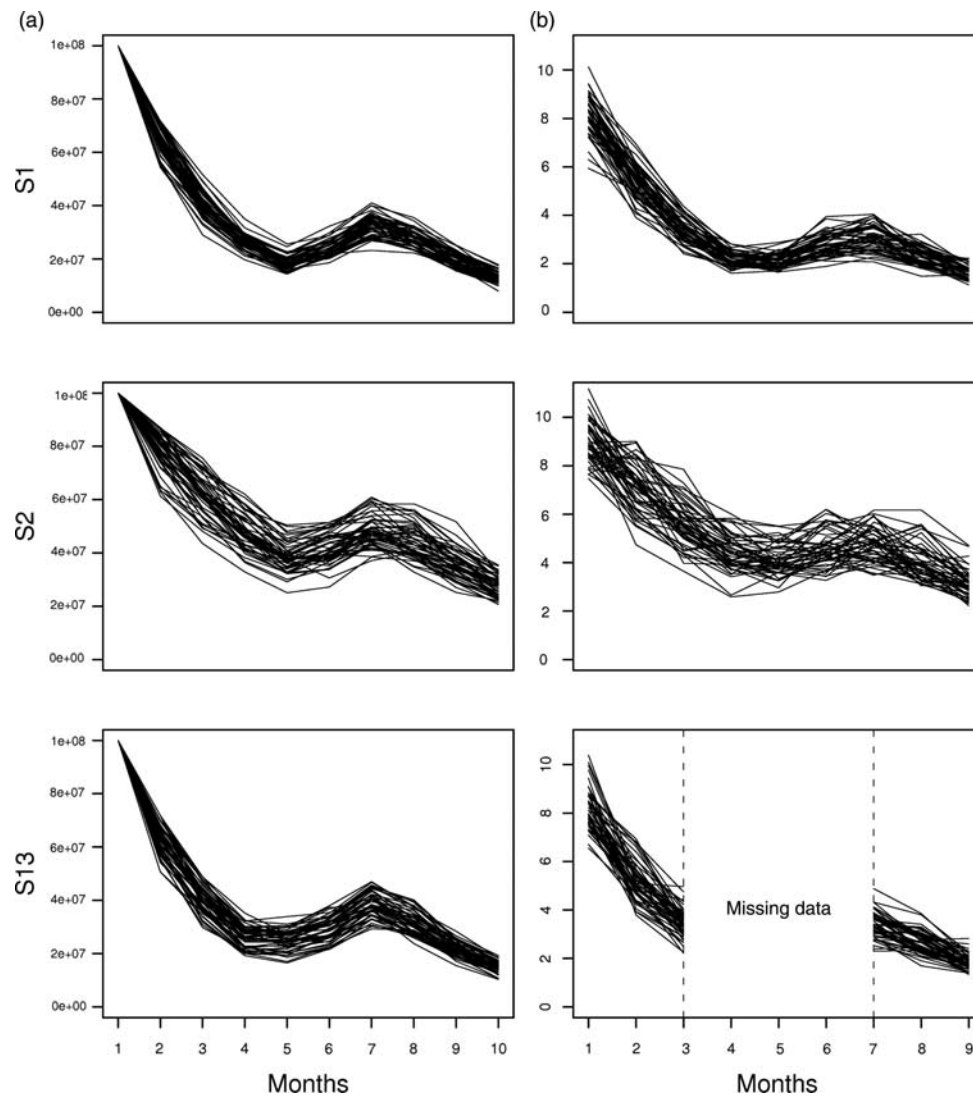
Figure 3. The SE approach, showing the shape of the 50 simulated trajectories for (a) abundance (in numbers), and (b) abundance indices (thousands per day at sea) for three representative scenarios S1, S2 (lower depletion), and S13 (fishing moratorium during months 4, 5, and 6).

depletion in the abundance index as a result of catch removals: 50 and 80% of the initial abundance was depleted after 3 and 10 months, respectively. M was fixed at 0.1, and $\{\lambda_t\}_{t=1, \ldots, n}$ peaked in April (Figure 1). Process and observation noise were moderate, with a 10% coefficient of variation ($CV_o = CV_p = 0.1$). The model used for the estimation phase is the same as that used for the simulation (same values of M), $\{\lambda_t\}_{t=1, \ldots, n}$, and the ratio of the process and observation error variances was fixed at 1. Catches and abundance indices were available for the 10 months, with no missing data. The prior distributions used were those defined in Table 2, and their mode (when it existed) corresponded to the value of the parameter used in the simulation.

Influence of the quantity of information in the dataset (S2–S5). We assessed the sensitivity of the inferences to two key factors that monitor the quantity of information in the data: the depletion rate (i_n/i_1), and the noise intensity σ^2. To address the sensitivity to depletion rate, we compared scenario S1 with scenario S2, characterized by a lower exploitation rate fixed at $h = 0.13$ month^{-1}, leading to a lower depletion rate (only 30% of the initial abundance depleted after 3 months, and 60% after 10 months). A

higher rate of natural mortality would lead to a faster depletion rate, but not necessarily to a more informative data configuration, because the proportion of the depletion attributed to catches would be smaller. To address this point, scenario S3 was built with all characteristics equal to S1, but with a higher natural mortality rate, $M = 0.2$. Two additional scenarios, S4 and S5, with increasing noise intensity ($CV = 0.20$ and 0.30, respectively) were compared with S1.

Sensitivity to the prior on N_1 (S6–S8). We assessed the sensitivity of the inferences to the choice of the prior on N_1. Scenarios S6–S8 used the same dataset as S1, but inferences were derived with different priors on N_1. In S6, the prior for N_1 is unbiased (mode = simulated value = 10^8), but it is weaker ($CV = 5$) than in S1. In S7 and S8, the models of the priors are biased by factor of $1/10$ or 10, respectively, from the simulated value.

Sensitivity to the mis-specification of M (S9 and S10). M cannot be estimated from these data, so must be set to a constant in the model. We assessed the sensitivity of setting M to an incorrect value in S9 and S10. In S9, simulations used $M = 0.2$ (data from S3), whereas the estimation was made with $M = 0.1$. In S10, the

Table 4. Prior distributions for the hierarchical models on the values of N_1 and q with or without autocorrelation.

Parameter	Distribution	
Exchangeable		
N_1	For $y = 1, \ldots, n$ $\log(N_1[y]) \sim$ normal $(\mu_{\log N}, \sigma^2_{\log N})$	$\mu_{\log N} \sim$ normal(20, $V = 100$) $\sigma_{\log N} \sim$ uniform(0, 10)
q	For $y = 1, \ldots, n$ $\log(q[y]) \sim$ normal $(\mu_{\log q}, \sigma^2_{\log q})$	$\mu_{\log q} \sim$ normal(-11.5, $V = 100$) $\sigma_{\log q} \sim$ uniform(0, 10)
With random walk		
N_1	For $y = 1, \ldots, n$ $\log(N_1[y]) \sim$ normal $(\mu_{\log N[y]}, \sigma^2_{\log N})$ with $\mu_{\log N[y+1]} \sim$ normal $(\mu_{\log N[y]}, \sigma^2_{\log N})$	$\sigma_{\log N} \sim$ uniform(0, 10) $\mu_{\log N[1]} \sim$ normal(20, $V = 100$) $\sigma_{\mu \log N} \sim$ uniform(0, 10)
q	For $y = 1, \ldots, N$ $\log(q[y]) \sim$ normal $(\mu_{\log q[y]}, \sigma^2_{\log q})$ with $\mu_{\log q[y+1]} \sim$ normal $(\mu_{\log q[y]}, \sigma^2_{\mu \log q})$	$\sigma_{\log q} \sim$ uniform(0, 10) $\mu_{\log q[1]} \sim$ normal(-11.5, $V = 100$) $\sigma_{\mu \log q} \sim$ uniform(0, 10)

same simulated data as in S1 were used ($M = 0.1$), but the estimations were made with $M = 0.2$.

Sensitivity to the rhythm of the secondary recruitment pulse (S11 and S12). The value $\{\lambda_t\}_{t=1, \ldots, n}$ cannot be estimated from the abundance index and catch data only, so must be fixed. However, as spawning season and growth rate of octopus vary year on year, the rhythm with which the secondary recruitment pulse arrives in the fishery is variable and uncertain. We assessed the sensitivity of the estimation method to mis-specification of λ. The data were simulated by using a series $\{\lambda_t\}_{t=1, \ldots, n}$ which is lagged 1 month earlier (S11) and 1 month later (S12) compared with the reference rhythm used for estimation.

Impact of missing data in the series of abundance indices (S13 and S14). In the Moroccan fishery, a fishing moratorium is set up during the breeding period. The measure aims to ensure a satisfactory level of recruitment for the following year. Months with $c_t = 0$ and $i_t = $ NA (not available) indicate that a fishing moratorium has been put in place. Scenarios S13 and S14 provide an assessment of the sensitivity of the inferences to the duration of the fishing moratorium. In S13, the moratorium is for months 4–6 (capturing situations observed in 2000), and in S14 in months 3–6 (capturing situations observed in 2001).

Sensitivity to the error structure (SSM, OBS, and PROC) (S15 and S16). Both S15 and S16 are based on the simulated data of S1 (operational model with both process noise and observation error). S1, S15, and S16 only differ in the error structure used during the fitting process. S15 corresponds to the OBS, where the model is fitted under the hypothesis of no process error ($\sigma^2_p = 0$, observation error only), and S16 to the PROC, where the model is fitted under the hypothesis of no observation error ($\sigma^2_o = 0$, process noise only).

Analysis of the 21 Moroccan depletion time-series

Five models of increasing complexity were applied to the Moroccan data, described in the following subsections.

All depletion time-series treated as independent

In the baseline model configuration, M_1, the 21 depletion time-series were treated independently with the model described in Equations (1) and (2), the fixed parameters M and λ used for the reference scenario S1 and the prior in Table 2.

Hierarchical structure

Based on the baseline model configuration M_1, four alternative hierarchical structures were designed, denoted as $M_2, \ldots, M_5$, in which the 21 depletion time-series were modelled jointly. In configuration M_2, we followed McAllister *et al.* (2004), and both the initial abundance for the 21 depletion series, the values of N_1 (with $y = 1, \ldots, 21$) and catchability q were modelled in an exchangeable hierarchical structure (Table 4).

In M_3–M_5, the hypothesis was introduced that the values of N_1 and q form an autocorrelated RW. The fishing efficiency is not likely to show abrupt changes with time, but rather to show fluctuations caused by gradual changes in behaviour and development of the fishing fleet. Therefore, the values of q were modelled as being drawn in a lognormal, with means (in log-scale) modelled as a normal RW (Table 4). Likewise, the values of N_1 are likely to show autocorrelated fluctuations because of the population dynamics and environmental influences. Hence, the values of N_1 were also modelled as lognormal with means (in log-scale) modelled as a normal RW (Table 4). Note that the variance parameter that underlies the RW is unknown, with a relatively uninformative prior on it. Hence, such models can fit abrupt changes in the series. In configuration M_3, RW is introduced only on the values of q, the values of N_1 being modelled as hierarchically exchangeable (Table 4). In M_4, RW is introduced on the values of N_1 only, the values of q being modelled as exchangeable. In M_5, an RW was introduced on values of both N_1 and q.

To provide a sensitivity analysis of the inferences to mis-specification of M and λ, the estimation procedure was also run with M set at 0.2 month^{-1}, and by considering a vector λ lagged 1 month back (i.e. earlier) and 1 month forward (later) compared with the baseline rhythm.

MCMC simulations

All computations were performed with the R platform (www.R-project.org). Given a series of catches $\{c_t\}_{t=1, \ldots, n}$ and abundance indices $\{i_t\}_{t=1, \ldots, n}$, the joint posterior distribution of all unknowns $p(N_{t=1, \ldots, n}, R, q, \sigma^2 |$data$)$ can be approximated via the MCMC simulation method. Here, the mechanisms of the MCMC simulations are not detailed. Instead, we refer the reader to Meyer and Millar (1999) and other applications (e.g. Rivot *et al.*, 2004; Hammond and Trenkel, 2005; Swain *et al.*, 2009), who showed how the Metropolis–Hastings within Gibbs
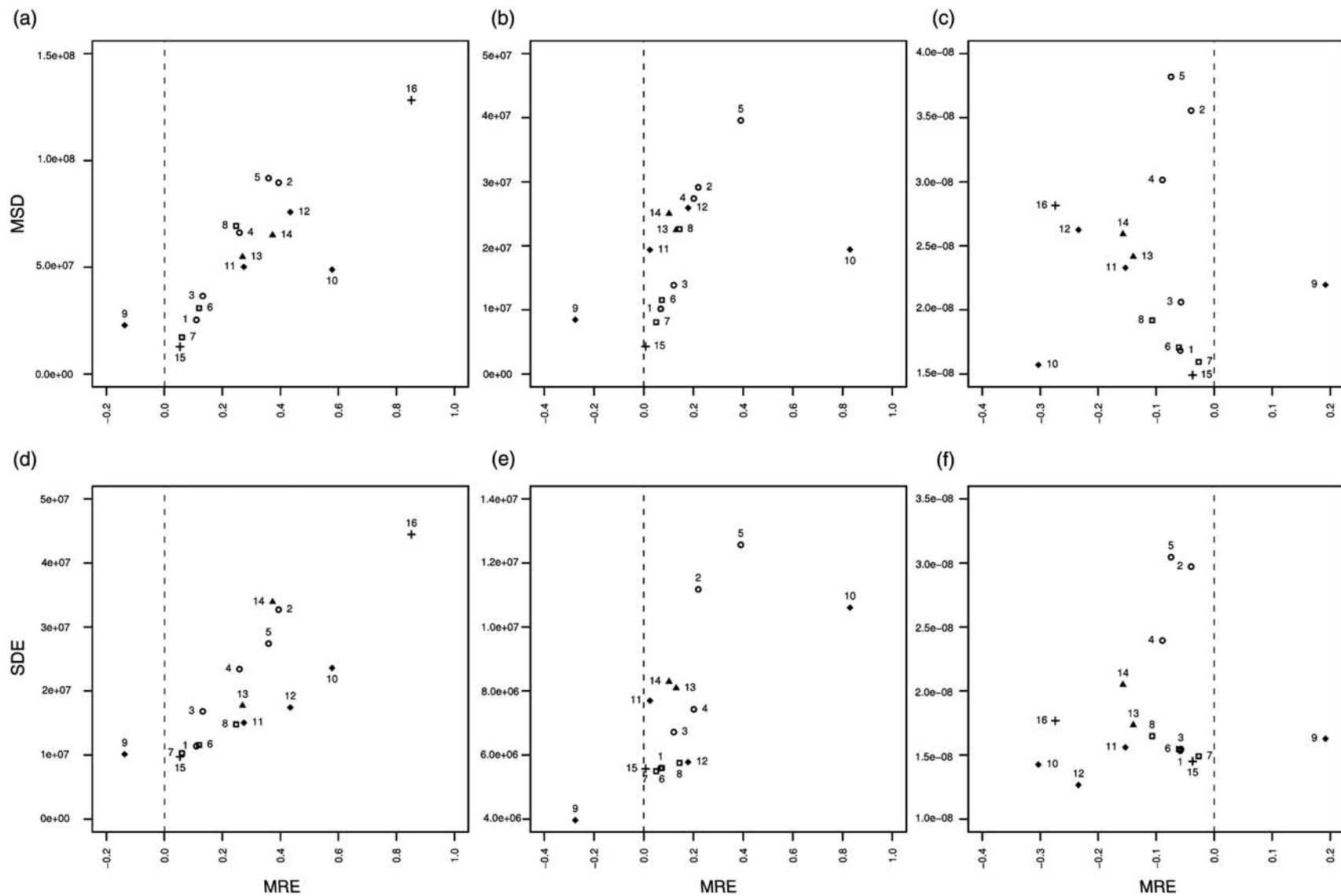
Figure 4. The SE approach, showing the performance of the estimation method measured on (a and d) N_1, (b and e) R, and (c and f) q, for the 16 scenarios tested. The performance is measured by MRE (*x*-axis) and MSD (*y*-axis, top panels), and SDE (*y*-axis, bottom panels). Scenarios are plotted using symbols related to the four issues they address. Open circles, influence of the quality of information in the dataset (S1, ..., S5); open squares, sensitivity to the prior on N_1 (S6, ..., S8); diamonds, sensitivity to mis-specification of M and λ_t (S9, ..., S12); triangles, sensitivity to the duration of the fishing moratorium (S13 and S14); crosses, observation error and process error methods (S15 and S16; the MRE, MSD, and SDE criteria for R in S16 are not shown because they are outside, i.e. highly positive values, the range of the graph).
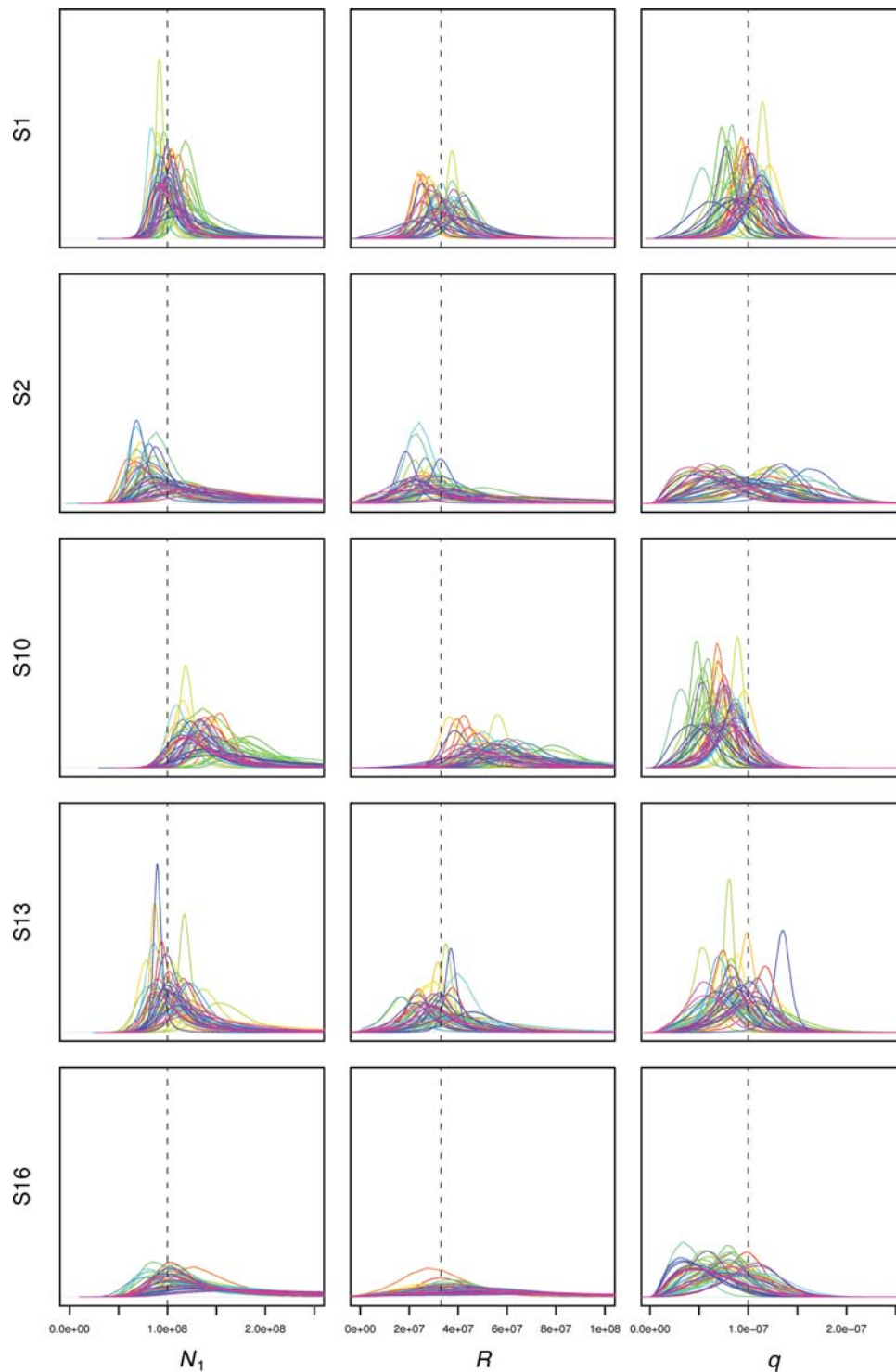
Figure 5. The SE approach, showing profiles of the marginal posterior probability distributions of key parameters N_1, R, and q for scenarios S1, S2 (lower depletion), S10 (mis-specification of $M = 0.2$), S13 (fishing moratorium during months 4, 5, and 6), and S16 (estimation under the process error model assumption). For each scenario and each parameter, 50 posterior distributions corresponding to 50 simulation trials are plotted. The vertical line represents the true values used in the simulations.

algorithm implemented in BUGS software family (Thomas *et al.*, 1992; Lunn *et al.*, 2009) can be used to fit non-linear non-Gaussian SSMs. All the Bayesian estimations (both the SE approach and the application to Moroccan data) were derived using the OpenBUGS 3.0.3 software (available at http://mathstat

.helsinki.fi/openbugs/) through the BRugs package, which allowed us to run OpenBUGS from the R platform.

For all estimations, three MCMC-independent chains with dispersed initialization points were used. For each chain, the first 100 000 iterations were discarded. After this "burn-in" period,

only one in 10 iterations was kept to reduce the MCMC sampling autocorrelation. Inferences were then derived from a sample of 30 000 iterations derived from three chains of 10 000 iterations. All the modelling results have undergone tests to assess convergence of MCMC chains (the Coda package of R). It is therefore assumed that the reported posterior probability density functions are representative of the underlying stationary distributions.

The calculation for the SE approach was time-consuming; each scenario (50 estimations procedure) took ~6 h (Processor Intel Duo-core 2Gz).

Results
SE approach
The MRE, MSD, and SDE values obtained for the three key parameters N_1, R, and q and for the 16 scenarios tested are summarized in Figure 4. The marginal posterior distributions of N_1, R, and q obtained for five contrasting scenarios are shown in Figure 5.

Inferences are sensitive to the quantity of information in the data
Results showed that the strength of the depletion at the start of the time-series critically determines the performance of the estimation method. Inferences are generally unbiased, precise, and reliable when the data show a strong depletion in response to catch removals. When depletion becomes weaker, identifiability problems appear between q and N_1, and the estimation may fail. Estimates of q are likely to be negatively biased, corresponding to positively biased estimates of N_1 and R. Comparison between the inferences obtained in S1 and S2 illustrates this general conclusion (Figure 4). Compared with S1, which provides the most information for parameter estimation, S2 leads to a 40 and 20% overestimate of N_1 and R, respectively. The inferences on q are also of poor quality. For the three parameters, the variance of the estimates is much higher for S2 than for S1, indicating that the inferences are less reliable (Figure 4). Comparison between S1 and S3 (Figure 4) shows that the data in S3 become less informative and the performance of the depletion method declines because more of the depletion is attributable to natural mortality and less to fishing. Estimation performance was sensitive to the intensity of noise in the data. Comparison between S1, S4, and S5 (Figures 4 and 5) illustrates how the quality of the inferences deteriorates with increasing noise intensity, in terms of biases, precision, and reliability.

Inferences are not sensitive to prior speciation on N_1
For a rather informative dataset characterized by a strong depletion rate, inferences are robust to the prior on N_1 (e.g. S1 vs. S6, S7, and S8). Even prior distributions with biased modes (S7 and S8) led to relatively unbiased and precise posteriors.

Sensitivity to mis-specification of M and λ is moderate to high
The performance of the estimation method can be reduced if M (natural mortality) and λ (the rhythm of the secondary recruitment) are mis-specified. Inferences appear to be highly sensitive to mis-specification of M. Results from S9 and S10 demonstrated that overestimating M in the estimation procedure (S10) resulted in positively biased estimates of N_1 (60%) and R (80%), and in negatively biased estimates of q (Figure 5). To a lesser extent, underestimating M (S9) results in underestimates of N_1 and R. The sensitivity to overestimating

M is because a larger value of M decreases the fraction of the depletion attributed to catch removal, so reduces the information in the data.

Mis-specification of λ seems to have less of an impact on the performance of the estimation (S1 vs. S11 and S12). Both R and N_1 are overestimated when λ is mis-specified, such that it is thought to occur too early (S11) or too late (S12), but the bias in R is always <20%.

Inferences remain accurate even with missing data
Comparing scenarios S1 with S13 and S14 shows that the performance of the estimation drops when the proportion of missing data increases. Yet, results suggest that if the depletion rate in the series of abundance indices is high, the performance remains relatively good. Reliable inferences are obtained even if the moratorium begins early in the fishing season (S14).

Performance of the three estimation methods, SSM, OBS, and PROC
The results demonstrate the very poor estimation performance of the PROC (S16). The bias is positive for N_1 and R, and negative for q, and is large for all three parameter estimates (Figure 4b and d). The MRE, MSD, and SDE criteria for R in S16 are not shown because they are outside the range of the graph. The posterior distributions of N_1, R, and q are widely dispersed (Figure 5), and the variance of the point estimates between the 50 simulations is also high. In contrast, the three criteria MRE, MSD, and SDE do not show clearly that the SSM method outperforms the OBS (S15). However, the MSD criterion (slightly lower for S15) combined with a precise examination of the shape of the posterior distributions (not shown) indicate that the OBS generally produces tighter (though not less biased) posterior distributions than the SSM method. In other words, the OBS produces more "incorrectly precise" distributions than the SSM method, so increasing the risk of deriving biased inferences. The SSM method produces more dispersed and slightly less biased posterior distributions, so appears to be a more robust inference approach in a context of multiple sources of uncertainty.

Conclusions
The performance of the BSSM estimation method was satisfactory under most conditions considered. In nearly all scenarios, biases on R rarely exceeded 40%. Inferences on N_1 and q were slightly more sensitive than those on R, with relative biases of N_1 that rarely exceeded 50%. Our results corroborate identifiability problems between q and N_1 (Gonzalez Cano and Restrepo, 2001; McAllister *et al.*, 2004; Magnusson and Hilborn, 2007) for non-informative data. Low depletion rates and/or high noise intensity lead to negatively biased and imprecise estimates of q, which in turn lead to positively biased estimates of N_1.

The octopus is intensely exploited in Moroccan waters, producing strong depletion rates during the fishing season (depletion rate is >70% for most fishing seasons; see Figure 2). Given the results of the SE analysis, the strong depletion in the Moroccan data may guarantee a good fit of the model for most of the 21 depletion series. In the second part of the series, fishing moratoria become more frequent. In particular, in the final three depletion series, only two time-steps are available, before a 3- or a 4-month closure. However, the results of the SE approach revealed that reliable inferences can be obtained even in such apparently data-poor situations.
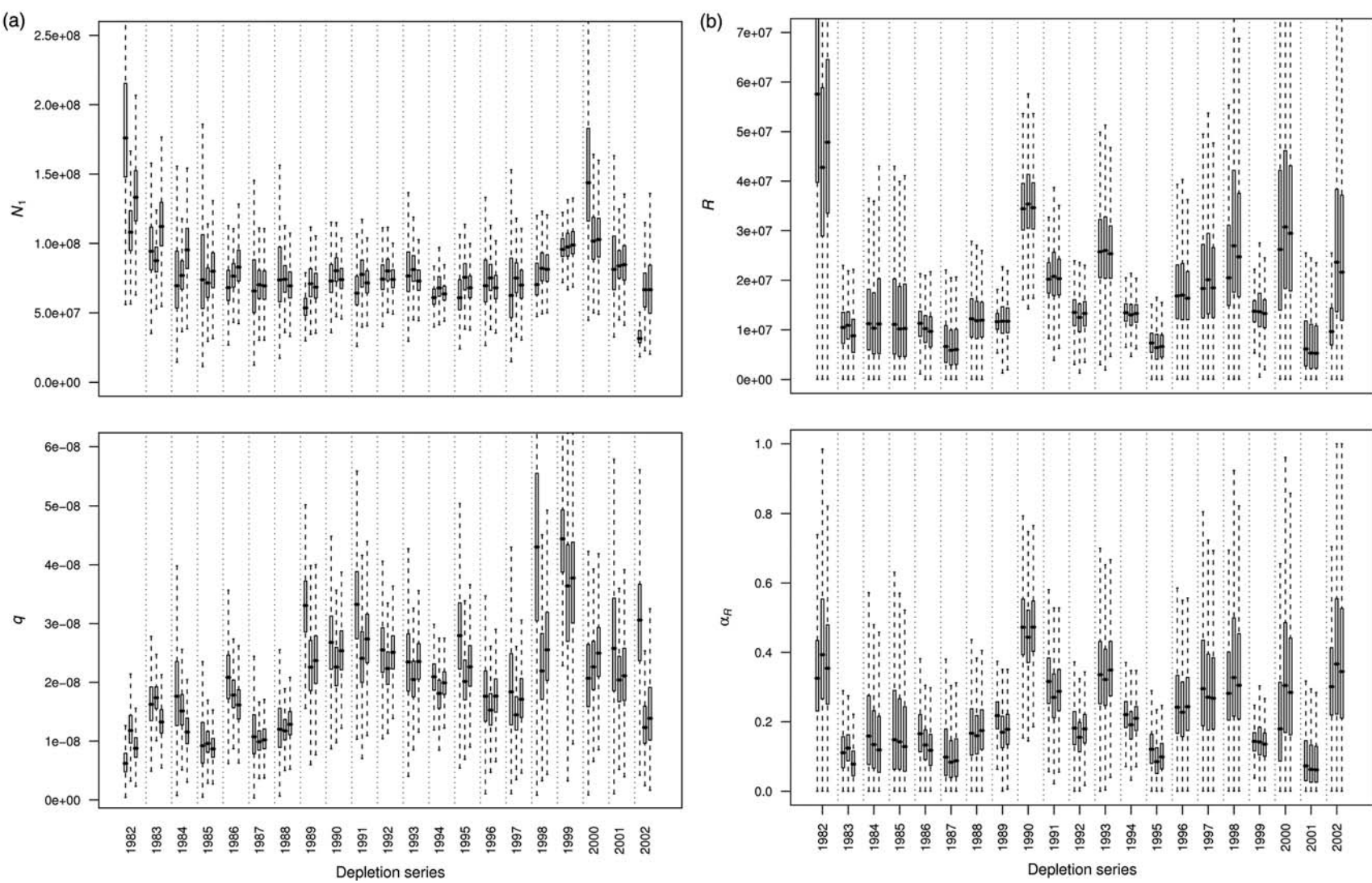
Figure 6. Analysis of the Moroccan dataset, showing the sensitivity of the inferences on (a) N_1 and q, and (b) R and α_R to the model configurations M_1, M_2, and M_5. For each of the 21 depletion series (x-axis), the three box-plots represent the posterior distributions obtained under the alternative model configurations in the following order: M_1, all depletion series are independent; M_2, exchangeable hierarchical structure on the values of N_1 and q; M_5, RW on the values of N_1 and q.
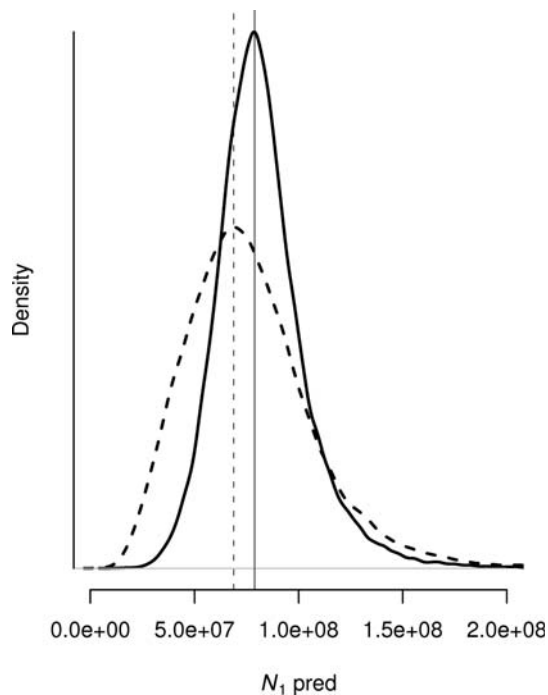
Figure 7. Analysis of the Moroccan dataset, showing posterior predictive distributions of the initial abundance N_1 derived from the exchangeable hierarchical model M_2 (solid line) and from the hierarchical model with RW M_5 (dotted line).

The SE findings also flag some potential problems that may arise in the analysis of the Moroccan dataset. For some depletion series (e.g. 1982–1983, 1985–1986), the depletion rate is low and one must interpret the inferences with caution. The results also show that the inferences on R and N_1 might be sensitive to mis-specification of M and the rhythm of the secondary recruitment λ. Therefore, our estimation method using fixed values for M and λ needs to be accompanied by a sensitivity analysis to these parameters. Note too that the performance of the estimation method deteriorates when noise in the process and the data increases. As no information on the amount of noise associated with the dataset is available, results have to be interpreted with caution.

Applications to the Moroccan dataset

Model M_1: all depletion series treated independently

For almost all depletion series, model configuration M_1 provides sensible inferences for key parameters. The uncertainty about the estimates is low except for the depletion series 1982 and 2000 (Figure 6a). Note, though, that the model provides quite precise estimates of N_1 even for the last 2 years characterized by many missing data as a result of a long fishery closure. The medians of the posterior estimates of initial abundance N_1 vary among years around an average of $\sim$80 million animals (Figure 6a), with auto-correlated variations in the time-series.

Marginal posterior distributions of q (Figure 6a) suggest great variability of this parameter among years. However, this consideration should be cognizant of the high negative correlation in the joint posterior distributions of (N_1, q).

The model also provides sensible estimates of the secondary recruitment R. The values of α_R are well estimated. On average,

the secondary recruitment is 22% of the principal recruitment (Figure 6b). The median of the posterior estimates of R varies among years around an average of $\sim$17 million animals (Figure 6b). The uncertainty about R is higher than the uncertainty about N_1, in particular for the depletion series 1982, 1998, 2000, and 2002. The joint posterior distributions of N_1 and R do not reveal strong correlation patterns (not shown).

The estimates of the CV vary around 0.20 (not shown). According to the results from the SE approach, such noise intensity in the process and observations should allow one to remain confident in the quality of the inferences.

Hierarchical models $M_2, \ldots, M_5$

Four alternative hierarchical structures were tested in the model configurations M_2, M_3, M_4, and M_5 (M_3 and M_4 are not shown). In model M_2, values of both N_1 and q were modelled in an exchangeable hierarchical structure. As expected from a hierarchical model (Rivot and Prévost, 2002; McAllister *et al.*, 2004), the estimates of N_1 and q dropped towards the overall mean compared with the estimates obtained from the configuration M_1 (Figure 6a). The shrinkage effect is higher for years with less informative depletion series (e.g. 1982 and 2000), the hierarchical model M_2 providing much less uncertain posterior inferences than M_1 on N_1. Setting a hierarchical structure on the values of N_1 and q has relatively little effect on the estimates of R and α_R (Figure 6b).

The posterior prediction for N_1 obtained from hierarchical model M_2 (Figure 7) reflects the amount of information provided by the data from all depletion series. It can be used as a prior to predict the initial abundance for an unsampled year. The mode is $\sim$0.75 $\times$ 10^8, with 50% of the probability between 0.68 $\times$ 10^8 and 0.93 $\times$ 10^8.

The key hypothesis behind the exchangeable hierarchical structure is that conditional on the hyperparameters, the values of N_1 are iid. However, the time-series of N_1 and q obtained from the exchangeable hierarchical model M_2 reveals fluctuations with positive lag-1 autocorrelation coefficients (0.15 and 0.20 for N_1 and q, respectively). As expected from this observation, models M_3, M_4, and M_5, which introduce RW in the time-series of the N_1 and q was preferred to the exchangeable hierarchical model M_2. Indeed, the deviance information criterion (Spiegelhalter *et al.*, 2002; Rivot *et al.*, 2008) computed for the four model configurations are, respectively, -311, -313, -315, and -318, indicating that M_5 can be expected to predict the data most accurately among the models tested.

The posterior estimates obtained from M_5 do not drastically differ from those of M_2 (Figure 6a and b). The posterior predictive distribution for N_1 obtained from M_5 (Figure 7) gives maximum credibility to slightly lower values of N_1. This is easily explained because of the lag-1 autocorrelation: the predicted N_1 for 2003 (the next but yet unsampled year) depends on the value of N_1 from the previous year (2002), which was slightly lower than the overall mean.

Total abundance and exploitation rates

The model provides abundance estimates for each month since 1982 (Figure 8a). The effect of secondary recruitment is visible on the time-series of estimated abundance within each season (see for instance 1990 and 1996). The time-series of point estimates of the principal and secondary recruitment pulses exhibit smooth fluctuations (Figure 8b).
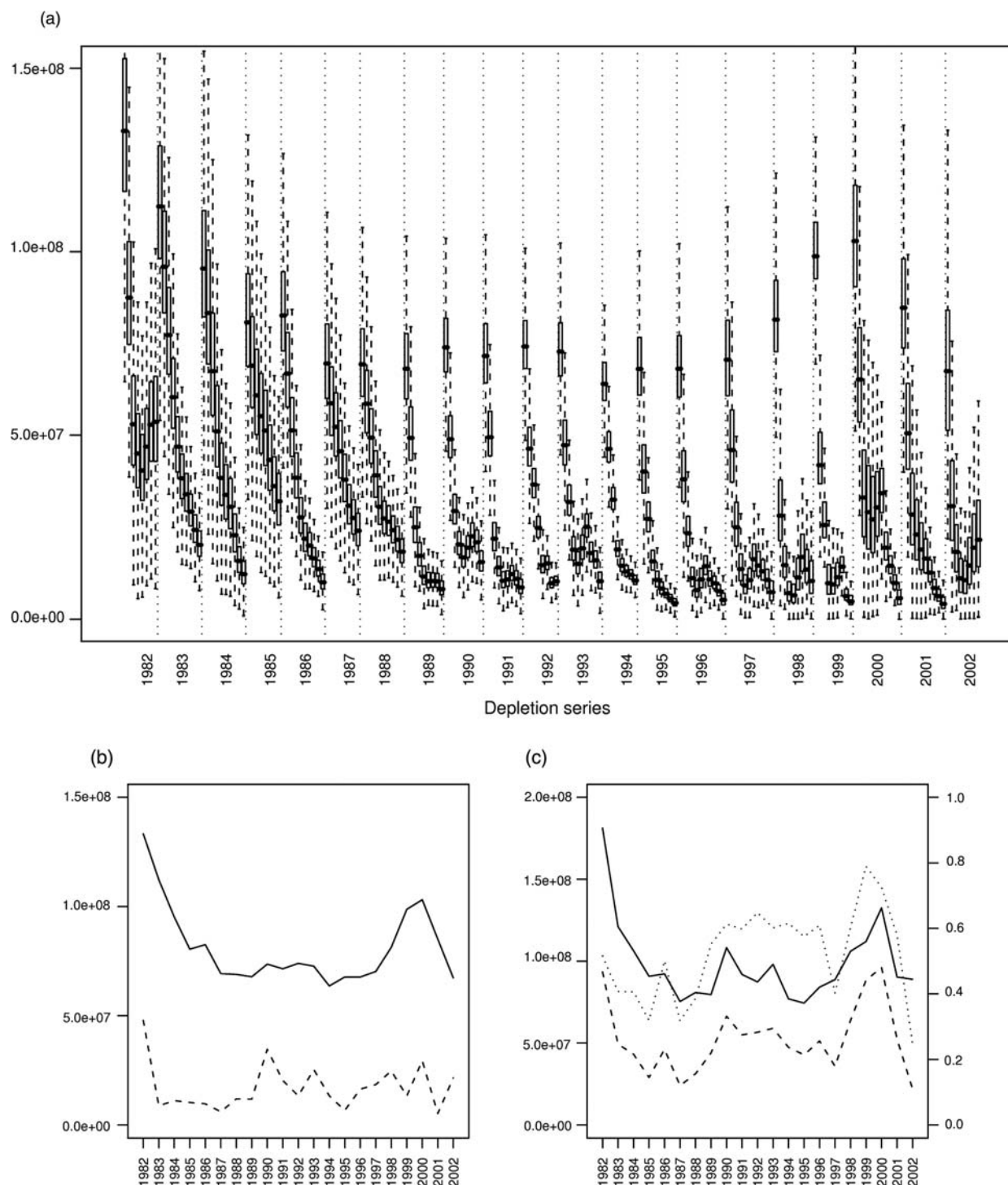
Figure 8. Analysis of the Moroccan dataset, showing the time-series (21 depletion series) of point estimates of N_1, R, and a comparison of the total recruitment with annual catches. (a) Box-plot of the posterior distributions of the number of octopus taken each month between 1982 and 2002; (b) Posterior medians of N_1 (solid line) and R (dashed line) by number; (c) Left axis (solid line), posterior medians of total recruitment $N_1 + R$ and total annual catches (dashed line) by number; right axis (dotted line), harvest rate estimated as the ratio of the annual catches vs. the posterior median of the total recruitment ($N_1 + R$).

Comparing the annual catches with estimates of total recruitment $(N_1 + R)$ allows us to estimate the exploitation rate. Estimated annual exploitation rates range from 25 to 80% (Figure 8c), consistent with earlier observations suggesting intense exploitation of octopus in Morocco (Faraj *et al.*, 2006). The exploitation rates exhibit a slightly increasing trend over the time-series, consistent with the expertise available to the fishery.
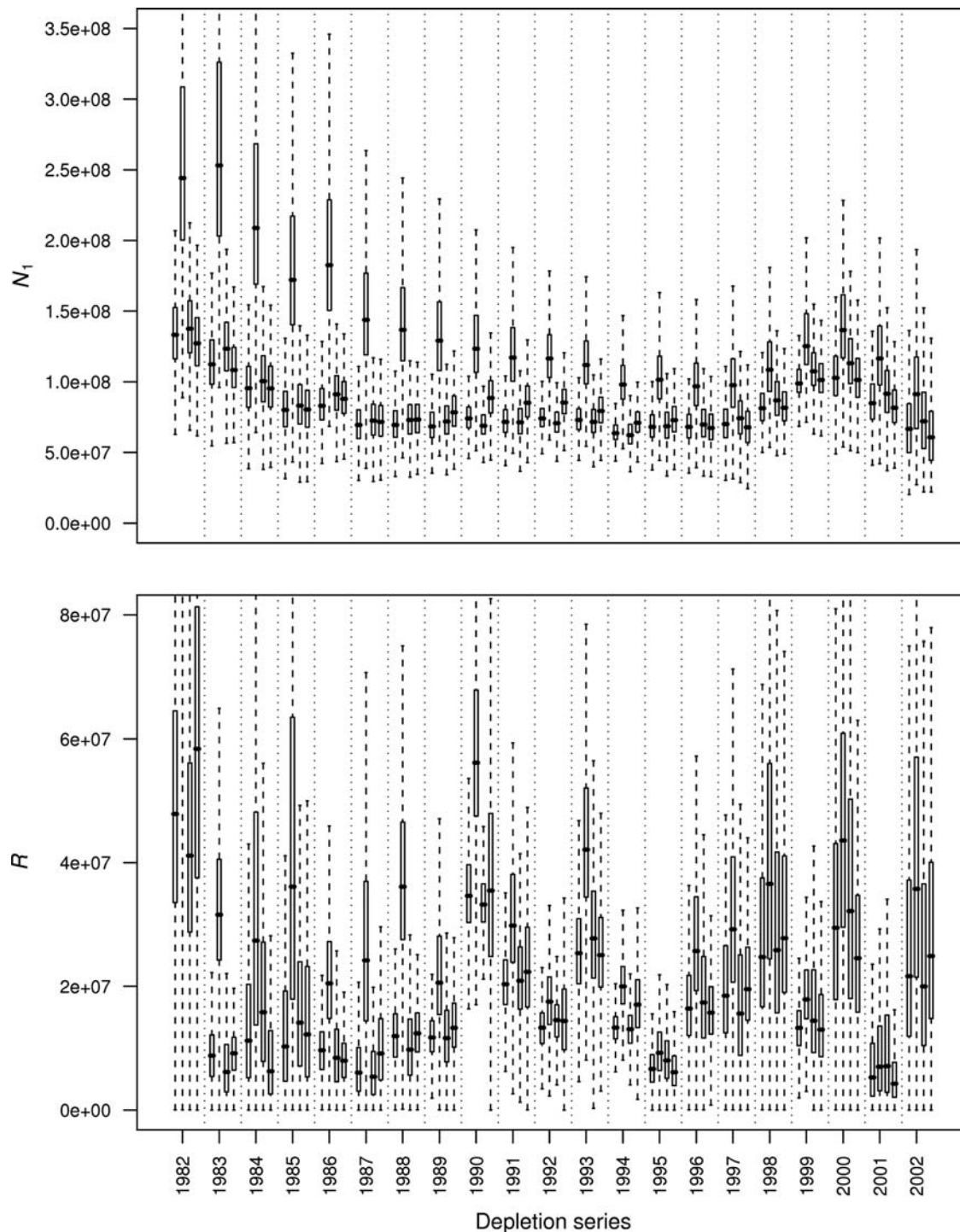
Figure 9. Analysis of the Moroccan dataset, showing the sensitivity of the inferences on N_1 and R to M and λ. For each of the 21 depletion series (x-axis), the four box-plots represent the posterior distributions obtained under four model configurations in the following order. First, M_5, RW on the values of N_1 and q, with $M = 0.1$ and baseline recruitment rhythm λ; second, M_5 with $M = 0.2$; third, M_5 with λ 1-month lagged earlier by reference to the reference rhythm; fourth, M_5 with λ lagged later by 1 month.

Sensitivity analysis in M_5

Conclusions relative to the sensitivity to M and λ are qualitatively the same as in the SE approach (Figure 9). The main caveat for the model is that inferences look very sensitive to the values of M. In contrast, for almost all years, the results look rather robust to changes in λ.

The sensitivity of the results to the prior on the key parameters N_1 and q was also checked by running model M_5 with weaker priors on N_1 and q (lognormal priors with $CV = 5$ rather than $CV = 2$). Inferences revealed insensitivity to these prior changes (not shown). We also checked whether the inferences were sensitive to the prior on the variance for the process and observation noise σ^2.

A uniform prior distribution on the interval (0, 100) was tested for σ^2. Inferences were robust to these prior changes (not shown).

Discussion
Strengths of the method

We believe that we have offered three substantial new contributions. First, to our knowledge, this work provides the first BSSM approach of the De Lury depletion model including both process and observation errors and an estimation of a secondary recruitment pulse. Second, an extensive evaluation of the sensitivity of a Bayesian version of this model to alternative model forms and data configuration is provided. Third, the Bayesian hierarchical approach of McAllister *et al.* (2004) was extended by introducing an RW formulation to capture the systematic fluctuations of the time-series of initial abundance and catchability.

The SE approach provides an analysis of the performance of the method and an evaluation of the reliability of the outputs of the model. SSM was considered to be the favoured default estimation method. Both process and observation errors are likely to be found simultaneously in real datasets, and the SSM approach outperformed the OBS and PROC in the presence of both sources of error. The results allowed us to quantify how the performance of the estimation method depended on the strength of the depletion attributable to catch removal in the first time-step of each fishing season. The stronger the depletion, the less the bias and the uncertainty in the estimation. Also, when the data were sufficiently informative, the depletion model provided accurate estimates of both the principal and the secondary recruitment pulses. Yet, inferences appeared to be sensitive to mis-specification of *M*.

The methodology was applied to the data of the Moroccan fishery over the 21 fishing seasons between 1982 and 2002. The strong depletion rates observed in the Moroccan data offer an informative data configuration for model fitting. The model was designed to account for a secondary recruitment pulse spread over a few months during spring (as in Royer *et al.*, 2002), in contrast to there being a single event (González-Yáñes *et al.*, 2006). To ensure that all parameters could be estimated, we followed the approach of Royer *et al.* (2002) and considered the recruitment rhythm to be known. It was defined from previous studies (Balguerías *et al.*, 2002) and the knowledge of local experts (AF, pers. obs.). Compared with Royer *et al.* (2002), who considered between-year variation in the recruitment rhythm, no data for between-year variation in λ were available so we were constrained to consider it as constant across years. However, our results were insensitive to mis-specification of λ. Although this could have resulted from the fact that *R* was low compared with the main recruitment, N_1, this outcome lends credibility to the estimates of the secondary recruitment pulse *R*.

Our analysis has provided estimates of hidden variables of important biological significance, such as annual recruitment (both primary and secondary) from 1982 to 2002, and estimates of the abundance each month. This, combined with catches, provides estimates of the annual exploitation rate. The estimates of high rates of exploitation presented here are consistent with previous findings (Faraj *et al.*, 2006). The between-year variability of the recruitment during the 1982–2002 time-series also suggests a strong influence of the environment (Pierce *et al.*, 2008), which merits future research.

The 21 depletion series in the Moroccan dataset were analysed using five alternative model structures of increasing complexity, ranging from model M_1 with all depletion series treated as independent to model M_5 where the values of N_1 and *q* were treated as autocorrelated time-series within a hierarchical model. The BHM offers an advantageous modelling strategy to analyse such datasets with similar depletion patterns each year (McAllister *et al.*, 2004). It organizes the transfer of information from years with informative data to years for which the data are less informative, improving the inference on non-informative years (Rivot and Prévost, 2002; McAllister *et al.*, 2004; Rivot *et al.*, 2008). We extended the hierarchical modelling framework by introducing RW on both N_1 and *q*. The model was the best compromise between quality of fit and complexity, and it allowed us to capture the smooth fluctuations in N_1 (and to a lesser extent in *q*). The smooth fluctuations in the values of N_1 may suggest a response to environmental variance.

Caveats and future improvements

Our model provides a framework for structuring further research and data collection.

Assumptions were made in the data preparation. In particular, total annual catches were disaggregated on a monthly time-step according to the monthly catch rhythm of the Moroccan industrial fleet. The assumption is realistic from 1982 to 1992, because the industrial fleet (Morocco and foreign countries) was the only one exploiting octopus then and operated throughout the year. The assumption is more questionable in the last 10 years (1992–2002), though, when artisanal and coastal operators entered the fishery. However, the industrial fleet still delivered 50–80% of the total landings. The data could be improved using catch and effort in monthly time-steps for the artisanal and coastal Moroccan fleets. However, the data were not available for the entire time-series, so we opted for a homogeneous approach for the whole time-series. Nevertheless, use of data from the artisanal fishery would be well worth considering in future.

The use of cpue as an index of abundance is also questionable, particularly because local effort could be positively correlated with local octopus abundance (Hilborn and Walters, 1992). As an improvement, standard statistical procedures such as generalized linear modelling could be used to extract the trend in abundance indices after having filtered other effects such as variability in size and/or horse power of trawlers (for examples, see Gascuel and Thiam, 1994; Gascuel *et al.*, 2007). Scientific surveys are carried out in Morocco (Faraj and Bez, 2007), but because they are not spatially or temporally homogeneous in the entire time-series, we also decided not to use their output in this first methodological approach. One could rely on the flexibility of the estimation framework to integrate such sources of data in the model.

To reduce the number of parameters and ensure statistical identifiability, the ratio of process vs. observation errors was fixed. However, in the absence of any information on the magnitude of process variability and observation noise, the ratio of variance was set at 1. This hypothesis is worth investigating further, though. Inferences on SSMs have seldom proved to be sensitive to the value of this ratio (Kimura *et al.*, 1996; Schnute and Kronlund, 2002; Punt, 2003), but SSM offers the advantages of independently integrating process and observation error, and more research is needed to help formulate more informative priors on the variances.

The SE approach and the sensitivity analysis showed that inferences are highly sensitive to assumptions on *M*. Little is known about the natural mortality of octopus in the wild. The

value of M was fixed at 0.1, which led to realistic mortality rates of ~45, 70, and 83% after 6, 12, and 18 months, respectively. The results showed that using $M = 0.2$ led to higher estimates of abundance. However, the value of $M = 0.2$ tested here for illustration has little biological significance, because it leads to an unrealistic mortality rate of ~70% after only 6 months. Hence, we believe that the illustrative sensitivity analysis overappraised the uncertainty of our results as a consequence of uncertainty about the value of M. It might be of interest to propose an alternative modelling strategy that better mimics true natural mortality processes. The octopus is a semelparous animal, so setting a constant rate of natural mortality appears to be a crude assumption. The model we proposed pools the two annual cohorts in the same dynamic equation, preventing the use of age-dependent mortality. For in-season stock assessment of the squid off the Falkland Islands, Agnew *et al.* (1998) used a multiple cohort approach, treating data as representing two distinct cohorts with their own dynamic equations. That approach allows definition of age-dependent rates of mortality. Building a two-cohort depletion model with age-dependent natural mortality (low mortality during the first months, increasing to a plateau in later months when reproduction starts) should be considered.

Some fixed hypotheses have been formulated about the parameter q. In particular, q has been considered to be constant between months within a fishing season. However, catchability at the start of the period is likely to be higher than at the end of the period owing to changes in the behaviour of the animals at the onset of reproduction (AF, pers. obs.). However, a modelling strategy of varying q should be used with caution because it would increase the number of unknowns to be estimated and therefore the risk of non-identifiability.

Time-series of recruitment for understanding the influence of the environment

The role of upwelling in the bottom-up control of marine ecosystems is well established: strengthening of the trade wind generates upwelling of deep, nutrient-rich water to the surface, producing optimal environmental conditions for plankton growth (Cury and Roy, 1989; Bakun, 1990; Cushing, 1990). Pelagic larvae of octopus should benefit from retention processes in enriched areas (Demarcq and Faure, 2000; Faure *et al.*, 2000; Otero *et al.*, 2008). Good survival of pelagic larvae should support high levels of recruitment (Rodhouse *et al.*, 1992; Bakun and Csirke, 1998; Waluda *et al.*, 1999). Previous studies have demonstrated the effects of sea temperature and retention processes on recruitment fluctuations in cephalopods: *Loligo gahi* in the South Atlantic (Agnew *et al.*, 2000), *Loligo forbesi* in the English Channel (Robin and Denis, 1999), *O. vulgaris* along the Galician coast (Otero *et al.*, 2008) and on the Saharan Bank (Demarcq and Faure, 2000; Balguerías *et al.*, 2002). The recruitment index provided here could be used further to investigate the influence of the upwelling regime on interannual variations in octopus population dynamics in the context of both medium- and long-term changes (Bakun, 1990; Santos *et al.*, 2005). However, there are clear distinctions between the spatial patterns of spawning and recruitment of the Moroccan stocks (Faraj and Bez, 2007), and more research is needed to integrate this spatial dimension into our Bayesian estimation approach.

Implications for management

Finally, the BSSM approach to stock assessment with a depletion model provides an integrated framework for data integration and prediction that accounts for multiple sources of uncertainty. It could therefore be applied to develop a predictive approach for decision-making and risk analysis. A depletion model applied on a weekly time-step is under development for in-season stock assessment and operational management of the Moroccan octopus fishery (Faraj *et al.*, 2006). The hierarchical BSSM approach developed here could be adapted to that weekly time-step if desired.

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