Hierarchical Bayesian approach for population dynamics modelling of fish complexes without species-specific data

Yan Jiao, Christopher Hayes, and Enric Corte´s

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Modelling the population dynamics of fish complexes is challenging, and many species have been assessed and managed as a complex that was treated as a single species. Two Bayesian state-space surplus production models with multilevel priors (hierarchical models) were developed to simulate variability in population growth rates of species in a complex, using the hammerhead shark complex (*Sphyrna* spp.) of the Atlantic and Gulf of Mexico coasts of the US as an example. The complex consists of three species: scalloped (*Sphyrna lewini*), great (*Sphyrna mokarran*), and smooth hammerhead (*Sphyrna zygaena*). Bayesian state-space surplus production models with multilevel priors fitted the hammerhead data better than a model based on single-level priors. The hierarchical Bayesian approach represents an intermediate strategy between traditional models that do not include variability among species, and highly parameterized models that assign an estimate of parameters to each species. By ignoring the variability among species, confidence intervals of the estimates of stock status indicators can be unrealistically narrow, possibly leading to high-risk management strategies being adopted. Use of multilevel priors in a hierarchical Bayesian approach is suggested for future hammerhead shark stock assessments and for modelling fish complexes lacking species-specific data.

Keywords: Bayesian hierarchical model, fish complex, hammerhead sharks, multilevel prior, uncertainty.

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Y. Jiao and C. Hayes: Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0321, USA. E. Cortés: National Marine Fisheries Service, Panama City Laboratory, Panama City, FL 32408, USA. Correspondence to Y. Jiao: tel: +1 540 2315749; fax: +1 540 2317580; e-mail: yjiao@vt.edu.

Introduction

A lack of data and an inability to identify individual species easily often preclude the development of species-specific assessments of fish stocks. It is therefore widely recognized that completion of species-specific assessments for many taxa will take time. Because of these difficulties, fish stock assessments have often had to focus on species aggregates, such as the large and small coastal shark complexes in the USA (Cortés, 2002a; SAFMC, 2006). Complex-based assessments, however, need to be improved before single-species stock assessments can be conducted, for the hammerhead complex and for other fisheries, such as those for the snapper–grouper complex in the US South Atlantic and Gulf of Mexico.

The current population dynamics models used for shark complexes are necessarily based on surplus production theory (e.g. SAFMC, 2006). Population growth rates of hammerhead sharks, for example, likely vary interspecifically as a result of different life-history traits or intraspecifically as a result of natural variability or methodological issues (Smith *et al*., 1998; Cortés, 2002b; Figure 1). Incorporating variability in productivity among species in a complex is problematic when using surplus production models. Here, we use a multilevel prior in a hierarchical approach to address the problem of simulating population growth rates and their associated uncertainty when multiple species are present and exhibit variability in productivity, yet that productivity cannot be assigned to a particular species. Models with multilevel priors are called hierarchical models even when the data are not hierarchically structured (Andrews *et al*., 1993; Roberts and Rosenthal, 2001; Gelman *et al*., 2004). Hence, we refer here to state-space surplus production models with multilevel priors to represent a situation without hierarchical data, but in which the model applied can be considered hierarchical. Multilevel priors have been used to represent species or group differences even when the data are not hierarchical and proven to be more robust than single-level priors (Andrews *et al*., 1993; Roberts and Rosenthal, 2001; Clark, 2003). In contrast to a model that is highly parameterized and that assigns a different parameter value to each species in a complex to capture changes in the population growth rate, hierarchical models accommodate species or group differences but assume that these differences derive from an underlying distribution (Clark, 2003; Wikle, 2003).

Hammerhead sharks (*Sphyrna* spp.) along the Atlantic and Gulf of Mexico coasts of the USA are managed as part of the large coastal shark complex and are used here as an example. Hammerhead sharks can also be considered as a complex of three species: scalloped (*Sphyrna lewini*), great (*Sphyrna mokarran*), and smooth hammerheads (*Sphyrna zygaena*). The current status of hammerhead sharks is of concern (Baum *et al*., 2003; Myers *et al*., 2007; Hayes, 2008). The scalloped hammerhead has been classified recently as globally endangered in the IUCN Red List, the smooth hammerhead as near threatened, and the great hammerhead as data deficient (IUCN, 2006). There are no estimates of population growth rates for great or smooth hammerheads, but they can be very different.

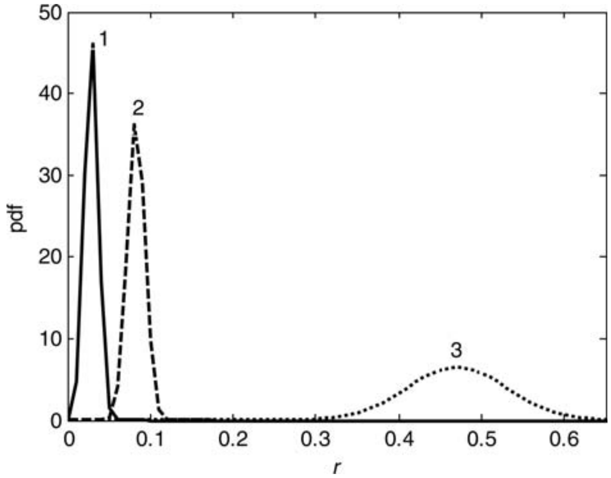

Figure 1. Three normal probability density functions (pdf) defined by means and variances from studies of the population growth rates (*r*) of scalloped hammerhead shark in the hammerhead shark complex. 1, Pacific scalloped hammerhead (30% of the *CV* is used here based on the mean value from Smith *et al.*, 1998); 2, Gulf of Mexico scalloped hammerhead (Cortés, 2002b); 3, Western Pacific scalloped hammerhead (Cortés, 2002a, b). There are no published studies on population growth rates of smooth or great hammerheads.

The hierarchically structured models were implemented in a Bayesian framework and analysed using Markov Chain Monte Carlo (MCMC) simulation. Bayesian approaches are used increasingly in assessing and managing fisheries stocks because of their flexibility in incorporating data from different sources, their ability to provide results for risk analyses of alternative management strategies, and because they incorporate prior knowledge of the fisheries into the assessment process.

Hammerhead data are limited because of their relatively low density in the ocean and because there is limited effort allocated to collecting data from both fishery-dependent and -independent sources. Demographic data help one understand the basis of population dynamics even when time-series of abundance or relative abundance exist and are especially useful when the populations are too sparse to assess (Kieth and Windberg, 1978; Krebs *et al.*, 2001). The use of demographic information to estimate population growth rates to be used as prior knowledge in a hierarchical framework helps us simulate the population dynamics of hammerhead sharks. Here, we used Bayesian models to address the variability among species through multilevel hierarchical priors and a time-varying, Bayesian hierarchically structured model to address the temporal variation in population growth rates caused by changes in species composition of the complex (Roberts and Rosenthal, 2001; Clark, 2003; Gelman *et al.*, 2004). The goodness-of-fit of the Bayesian hierarchical surplus production models is compared with that of the more classical Bayesian non-hierarchical surplus production model used, for example, for the large coastal shark complex stock assessment (SAFMC, 2006).

Methods

Data sources

Detailed descriptions of the data sources are available in Beerkircher *et al.* (2002), Cortés and Neer (2005a, b), Cortés *et al.* (2005), Ingram *et al.* (2005), and NMFS (2006) but a summary is given here.

Commercial landings data were obtained from two data-collection programmes run by the National Marine Fisheries Service (NMFS) that gather data directly from seafood dealers located in states on the US east coast and Gulf of Mexico. Estimates of dead hammerhead sharks discarded by pelagic longline fisheries targeting tuna and tuna-like species were obtained from the logbooks completed by pelagic longline and other vessels (the NMFS Pelagic Longline Logbook programme, PLL) and observer reports from the same fisheries (the NMFS Pelagic Longline Observer Programme, PLLOP). Recreational catch estimates were obtained from three data-collection programmes: the Marine Recreational Fishery Statistics Survey (MRFSS) and the Headboat Survey, both operated by NMFS, and the Texas Parks and Wildlife Department (TPWD) Recreational Fishing Survey, operated by the state of Texas. The MRFSS has been sampling private boat owners and charterboats operating in all coastal US states since 1981. Catch estimates used in our analyses included total catch (A + B1, where A is the fish brought ashore and available for identification to interviewers, and B1 is the fish not brought ashore whole but used as bait or discarded dead). The Headboat Survey samples headboats from North Carolina to Louisiana, and catch estimates for sharks are available since 1986. Catch estimates from the TPWD Survey, which samples private boats and charterboats in Texas, are available from 1986 (Figure 2).

Time-series of relative abundance were available from four sources: the NMFS Mississippi Laboratories bottom-longline shark survey (NMFS-SE), PLL, PLLOP, and the directed shark fishery bottom-longline observer programme (BLLOP). Since 1995,

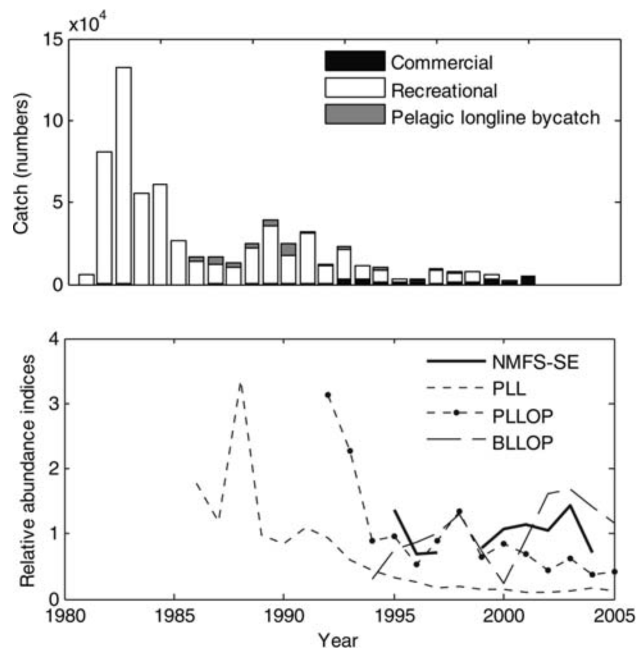

Figure 2. Summary of hammerhead shark complex fishery data. Top panel, catch composition; bottom panel, relative abundance indices. NMFS-SE, NMFS Mississippi Laboratories bottom-longline shark survey; PLL, NMFS pelagic longline logbook programme; PLLOP, NMFS pelagic longline observer programme; BLLOP, directed shark fishery bottom-longline observer programme.

the NMFS-SE survey has used a stratified random sampling design to monitor the distribution and abundance of coastal sharks throughout the Gulf of Mexico, the Caribbean, and the western North Atlantic. The PLL collects information through mandatory logbooks completed by longline and other fishing vessels landing swordfish in the US Atlantic, the Gulf of Mexico, and the Caribbean. Set-specific catch and effort data were available for the period 1986–2005. The PLLOP, in operation since 1992, covers approximately the same geographic area as the PLL, and 5% observer coverage of pelagic surface longline vessels was mandated in 1992, rising to 8% in 2002. Sharks represent ∼25% of the catch. The BLLOP places scientific observers aboard vessels of the directed shark fishery. Initiated in 1994 on a voluntary basis, it became mandatory for vessels with directed shark fishing permits in 2002 (Figure 2).

The four time-series of relative abundance were standardized using a generalized linear modelling approach derived from Lo *et al*. (1992), which assumes a delta lognormal model distribution. A binomial error distribution was first used to model the proportion of positive sets with a logit link function, then a lognormal error distribution was used to model the catch rates of positive (successful) sets (see Cortés *et al*., 2007, for a full description).

Hierarchically structured Bayesian surplus production models

Because the data available on hammerhead sharks were not size-, age-, or stage-structured, we used a state-space surplus production model as the basic model structure:

$$E(N_{t+1}) = N_t + G_t - C_t,$$
$$E(I_{i,t}) = q_i N_t, \qquad (1)$$

where N_t is the population abundance in year t, G_t the production function of the population in year t, C_t the total catch in year t, and q_i the catchability coefficient for the ith type of relative abundance index I_i. Here, we used the Schaefer model $G_t = rN_t\,(1 - N_t/K)$ as the production function; it is used widely in fisheries and ecology (May *et al*., 1979; Hilborn and Walters, 1992). In the Schaefer model, r is the population growth rate and K the carrying capacity. Instead of assuming a constant population growth rate in the Schaefer model, a hierarchically structured prior was used to model the population growth rate:

$$\begin{aligned} G_t &= rN_t\left(1 - \frac{N_t}{K}\right) \\ r &\sim N(\bar{r}, \sigma_1^2) \\ \bar{r} &\sim N(a, \sigma_2^2) \\ K &\sim U(a_1, a_2). \end{aligned} \qquad (2)$$

This was done to incorporate possible differences among, or hierarchy of, the population growth rates of the three species in the complex, as well as potential intraspecific variability. The hierarchical population structure is implied in the model through a multilevel prior of r. First, the intrinsic rate of population growth, r, of the species complex was assumed to follow a normal distribution, with mean $\bar{r}$ and variance σ_1^2. The first-level prior takes into account the randomness caused by intraspecific variability, but the data collected are assumed to derive from a single population or species because of the lack of species-specific data. However, r can also vary among species or populations, so we introduce the hyperparameters $\bar{r}$ and σ_1^2, where $\bar{r}$ can be considered the "mean" growth rate across different species or populations of the hammerhead complex and is assumed to follow a normal distribution with mean $a = 0.0661$ and standard deviation $\sigma_2 = 0.0996$. These values are based on summarized information on the population growth rate of 80 species or populations of shark (Hoenig and Gruber, 1990; Cailliet *et al*., 1992; Sminkey and Musick, 1995; Smith *et al*., 1998; Cortés, 2002b; Mollet and Cailliet, 2002; SAFMC, 2006). The carrying capacity of the complex, K, was assumed to follow a uniform distribution, with lower bound a_1 and upper bound a_2. The maximum observed catch was used as the value of a_1, and the estimated carrying capacity of the large coastal shark complex, 35 677 000 sharks, was used as the upper bound, a_2 (SAFMC 2006).

From an evolutionary perspective, the species used in this study may derive from a common ancestor and have similarities in population growth rates. We would therefore expect the parameters associated with each species or population to be similar to each other, allowing us to "borrow strength" from other species or populations to estimate r for the hammerhead shark complex.

We also developed a time-varying, hierarchical state-space surplus production model:

$$\begin{aligned} G_t &= rN_t\left(1 - \frac{N_t}{K}\right) \\ r_t &\sim N(\bar{r}, \sigma_1^2) \\ \bar{r} &\sim N(a, \sigma_2^2) \\ K &\sim U(a_1, a_2). \end{aligned} \qquad (3)$$

Here, the population growth rate of the species complex was allowed to vary annually, i.e. the annual data on population growth rate were treated as hierarchical (Jiao *et al*., in press). Potential variation in population growth rates among the three species can be represented as overall variation in the population growth rate over time as a consequence of temporal changes in species composition.

We used the observation-process error estimator, which considers both the process error in the function of population size and the observation error in the function of abundance indices (Millar and Meyer, 2000). The process error associated with the production and population dynamics equations is critical, especially for modelling the complex, which likely has more-complicated population dynamics characteristics than the individual species. Recent research comparing the observation-error estimator and the observation-process-error estimator also suggests the importance of using the observation-process-error estimator (De Valpine and Hasting, 2002).

Both lognormal and gamma error structures were investigated. If a lognormal error structure was used for both process and observation errors, the log-transformed population abundance $\ln(N_t)$ followed a normal distribution, with mean $\ln(N_t + G_t - C_t)$ and variance σ_N^2, and the log-transformed relative population abundance $\ln(I_{i,t})$ followed a normal distribution with mean $\ln(q_i N_t)$ and variance σ_{Ii}^2. The time-series of stock abundance is estimated by projecting the abundance forward from the start of the catch series (1981) with the history of annual catches, the abundance at the beginning of the fishery, N_{1981}, and r, $\bar{r}$, σ_1, K, q_i, σ_N, and σ_{Ii} as parameters (Quinn and Deriso, 1999).

If a gamma error structure was used for both process and observation errors, population abundance N_t followed a gamma distribution $G(\alpha_N, \beta_N)$, with mean $N_t + G_t - C_t = \alpha_N\beta_N$ and variance $\alpha_N\beta_N^2$, relative population abundance $I_{i,t}$ followed a gamma distribution with mean $q_iN_t = \alpha_{Ii}\beta_{Ii}$ and variance $\alpha_{Ii}\beta_{Ii}^2$. To further examine the results from different models and error distributions, the expected and observed relative abundance indices were compared.

Under the assumption of logistic population growth, $N_{\rm MSY} = rK/4$ and $F_{\rm MSY} = r/2$, where $N_{\rm MSY}$ is the abundance at maximum sustainable yield (MSY) from a production model, and $F_{\rm MSY}$ is the rate of fishing mortality at MSY. The estimated rate of fishing mortality F relative to $F_{\rm MSY}$, $F/F_{\rm MSY}$, the population size relative to $N_{\rm MSY}$, $N/N_{\rm MSY}$, and depletion, the most recent year's population size relative to K, were also compared among different models. The probability of F being greater than $F_{\rm MSY}$, i.e. $P(F > F_{\rm MSY})$, was used to define the risk of overfishing, and the probability of N being smaller than $N_{\rm MSY}$, i.e. $P(N < N_{\rm MSY})$, was used to define the risk of a population being overfished. $P(F > F_{\rm MSY})$ and $P(N < N_{\rm MSY})$ were estimated as the number of iterations where the posterior value of $F > F_{\rm MSY}$, and the number of iterations where the posterior value of $N < N_{\rm MSY}$ in a Bayesian approach (see explanation of the Bayesian approach below).

Bayesian approach and priors

Currently only Bayesian methods are computationally possible for a process–observation error model, and traditional maximum likelihood methods cannot solve it unless some assumptions are made for the process error (De Valpine and Hasting, 2002). The Bayesian approach uses a probability rule (Bayes' theorem) to calculate a posterior distribution from the observed data and a prior distribution, which summarizes the prior knowledge of the parameters (Berger, 1985; McAllister and Kirkwood, 1998; Gelman *et al.*, 2004). The Bayesian approach was used to estimate both the uncertainty in parameter estimates and population abundance. A non-hierarchical Bayesian model describes a posterior density for parameters ($p(\theta|I_i)$) using Bayes' theorem as

$$p(\theta|I_i) = \frac{\prod_{t=1}^{n} f(N_t|\theta)\prod_{t=1}^{n} f(I_{i,t}|\theta)\pi(\theta)}{\int_{-\infty}^{+\infty}\prod_{t=1}^{n} f(N_t|\theta)\prod_{t=1}^{n} f(I_{i,t}|\theta)\pi(\theta)\mathrm{d}(\theta)}, \quad (4)$$

whereas the hierarchical Bayesian method assigns priors of hyperparameters to yield the joint posterior

$$p(\theta' = \theta, \bar{r}, \sigma_1|I_i) = \frac{\prod_{t=1}^{n} f(N_t|\theta')f(I_{i,t}|\theta')\pi(\theta'|\bar{r}, \sigma_1)u(\bar{r})v(\sigma_1)}{\int_{-\infty}^{+\infty}\prod_{t=1}^{n} f(N_t|\theta')f(I_{i,t}|\theta')\pi(\theta'|\bar{r}, \sigma_1)u(\bar{r})v(\sigma_1)\mathrm{d}(\theta')}. \quad (5)$$

In the equations above, $f(N_t|\theta)$ is the probability density function of N_t given parameter vector θ, $f(I_{i,t}|\theta)$ is the probability density function of $I_{i,t}$ given parameter vector θ, and $u(\bar{r})$ and $v(\sigma_1)$ are the probability density functions of $\bar{r}$ and σ_1.

Bayesians believe that model parameters are random and that uncertainties in parameter estimation reflect the likelihood of a hypothesis that a parameter has a certain value (Hilborn *et al.*, 1993). We used WinBUGS software, a numerically intensive software package that implements general Bayesian models using "Metropolis–Hastings within Gibbs sampling" (Gilks, 1996; Spiegelhalter *et al.*, 2004). A detailed description of the "Metropolis–Hastings within Gibbs sampling" algorithm for the state-space surplus production model can be found in Millar and Meyer (2000).

Bayesian implementation of these models requires specification of prior distributions on all unobserved quantities. In general, non-informative priors (here, wide uniform distributions) were used for variances σ_1^2, σ_N^2, and σ_{Ii}^2. The prior for N_{1981} followed a uniform distribution with the lower bound equal to 1% of K, and the upper bound equal to K.

A critical issue in using MCMC methods is how to determine when random draws have converged to the posterior distribution. Here, three methods were considered: monitoring the trace for key parameters, diagnosing the autocorrelation plot for key

Table 1. Estimates of key parameters under three sensitivity scenarios for (top panel) Bayesian state-space surplus production models with a multilevel prior and (bottom panel) Bayesian state-space surplus production models.

Parameters	S1	S2	S3
	Indices: NMFS-SE + PLL + BLLOP **Prior of $\bar{r} \sim N$ (0.0661, 0.0996)**	**Indices: NMFS-SE + PLLOP + BLLOP** **Prior of $\bar{r} \sim N$ (0.0661, 0.0996)**	**Indices: NMFS-SE + PLL + BLLOP** **Prior of $\bar{r} \sim N$ (0.0661, 5 × 0.0996)**
r	0.32, 0.30, (−0.02, 0.79)	0.33, 0.31, (−0.02, 0.81)	0.34, 0.32, (−0.02, 0.81)
$\bar{r}$	0.13, 0.14, (−0.42, 0.68)	0.13, 0.14, (−0.43, 0.67)	0.22, 0.23, (−0.76, 1.16)
K	424, 352, (180, 1 083)	390, 331, (172, 924)	405, 341, (177, 1 062)
N_{1981}	334, 282, (120, 852)	299, 256, (99, 724)	322, 276, (115, 826)
$F_{2005}/F_{\rm MSY}$	1.62, 1.35, (0.44, 4.85)	1.33, 1.11, (0.25, 4.04)	1.57, 1.32, (0.42, 4.46)
$N_{2005}/N_{\rm MSY}$	0.15, 0.14, (0.06, 0.32)	0.20, 0.17, (0.07, 0.56)	0.15, 0.14, (0.06, 0.32)
	Prior of $r \sim N$ (0.0661, 0.0996)	**Prior of $r \sim N$ (0.0661, 0.0996)**	**Prior of $r \sim N$ (0.0661, 5 × 0.0996)**
r	0.25, 0.25, (−0.01, 0.55)	0.28, 0.27, (0.01, 0.58)	0.31, 0.30, (0.02, 0.64)
K	485, 394, (216, 1 388)	417, 352, (197, 987)	402, 360, (202, 837)
N_{1981}	375, 316, (146, 1 016)	302, 267, (117, 685)	315, 285, (133, 667)
$F_{2005}/F_{\rm MSY}$	1.29, 1.20, (−5.07, 7.94)	1.24, 1.14, (−5.78, 7.42)	1.32, 1.77, (−4.89, 6.95)
$N_{2005}/N_{\rm MSY}$	0.14, 0.13, (0.06, 0.26)	0.15, 0.14, (0.06, 0.32)	0.14, 0.13, (0.07, 0.27)

Results are based on the assumption of lognormal error structures. Mean, median, and 2.5% and 97.5% percentiles are given in parenthesis.

parameters, and using the Gelman and Rubin statistic (Gelman and Rubin, 1992; Spiegelhalter *et al.*, 2004). A detailed description of the use of these methods in fisheries can be found in Su *et al.* (2001). We used three Markov chains. The three chains converged after 50 000 iterations with a thinning interval of 5, based on the convergence criteria, and were discarded. A thinning interval of 5 was subsequently used to avoid parameter autocorrelation. Another 20 000 iterations were used to generate the posterior distributions. The posterior distributions of the key parameters were obtained through a kernel smooth approach (Bowman and Azzalini, 1997). The computing code is available upon request or online at http://filebox.vt.edu/users/ yjiao/complexcodes.

Table 2. Goodness-of-fit of the time-varying hierarchical Bayesian state-space surplus production model, the Bayesian state-space surplus production model with a multilevel prior, and the Bayesian state-space (SS) surplus production model for hammerhead shark complex data.

Models	DIC					
	Lognormal errors			Gamma errors		
	S1	S2	S3	S1	S2	S3
Time-varying hierarchical state-space surplus production	18.85	13.93	18.41	26.03	29.58	25.58
State-space surplus production with multilevel prior	27.52	36.38	28.28	34.84	37.24	34.65
State-space surplus production	43.59	45.33	43.41	34.73	40.99	34.69

Priors for r when non-hierarchical state-space surplus production models were used were N (0.0661, 0.0996) in S1 and S2, and N (0.0661, 5 × 0.0996) in S3. See Table 1 for a description of the scenarios.

Sensitivity analysis

Because of uncertainty in the various sources of relative abundance data used, the sensitivity of model outcomes, the robustness of the results to the data sources, was tested through different combinations (scenarios) of the relative abundance sources. The PLL and PLLOP are from the same fishery; although it is generally believed that data collected by observer programmes are more reliable than those from logbooks, the PLLOP series was shorter than, and showed some discrepancies with respect to, the PLL series. We therefore compared results from including either the PLL (scenario S1) or the PLLOP (scenario S2) series in the analysis (Table 1). To test the sensitivity of results to the hyperpriors, we extended the variance of hyperprior σ_1 to be 5× that in scenario 1 (scenario S3; Table 1).

The sensitivity of the model outcomes to the specified priors was tested through a comparison of the informative prior of $\bar{r}$ in the hierarchical models and the r in the non-hierarchical models (Tables 1 and 2).

Model goodness-of-fit

The goodness-of-fit of the Bayesian hierarchical surplus production model was compared with the classically used non-hierarchical surplus production model based on the estimates of the deviance information criterion (DIC):

$$\begin{aligned} \mathrm{DIC} &= 2\bar{D} - \hat{D} \text{ or } \bar{D} + p_D \\ D(y,\theta) &= -2 \log \mathrm{Likelihood}(y|\theta) \\ p_D &= \bar{D} - \hat{D}, \end{aligned} \tag{6}$$

where D is deviance, a measurement of prediction goodness for our models, p_D the effective number of parameters in a Bayesian

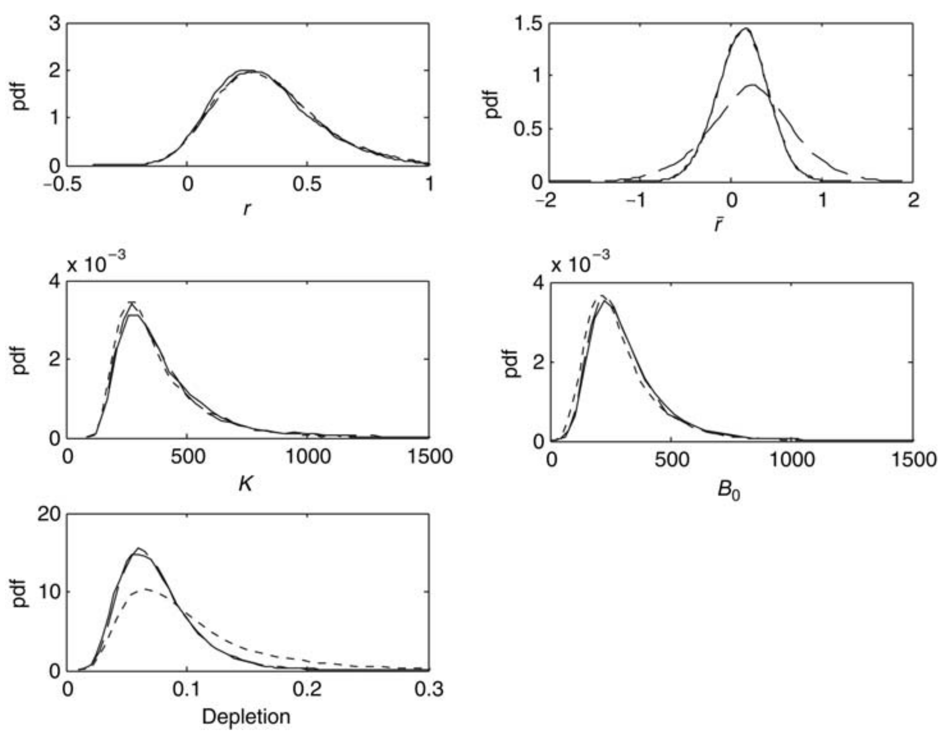

Figure 3. Probability density functions (pdf) of key parameters from the Bayesian state-space surplus production model with a multilevel prior of population growth rate ($\bar{r}$). Solid line, scenario S1; dotted line, S2; dashed line, S3. K and B_0 are in thousands of individuals.

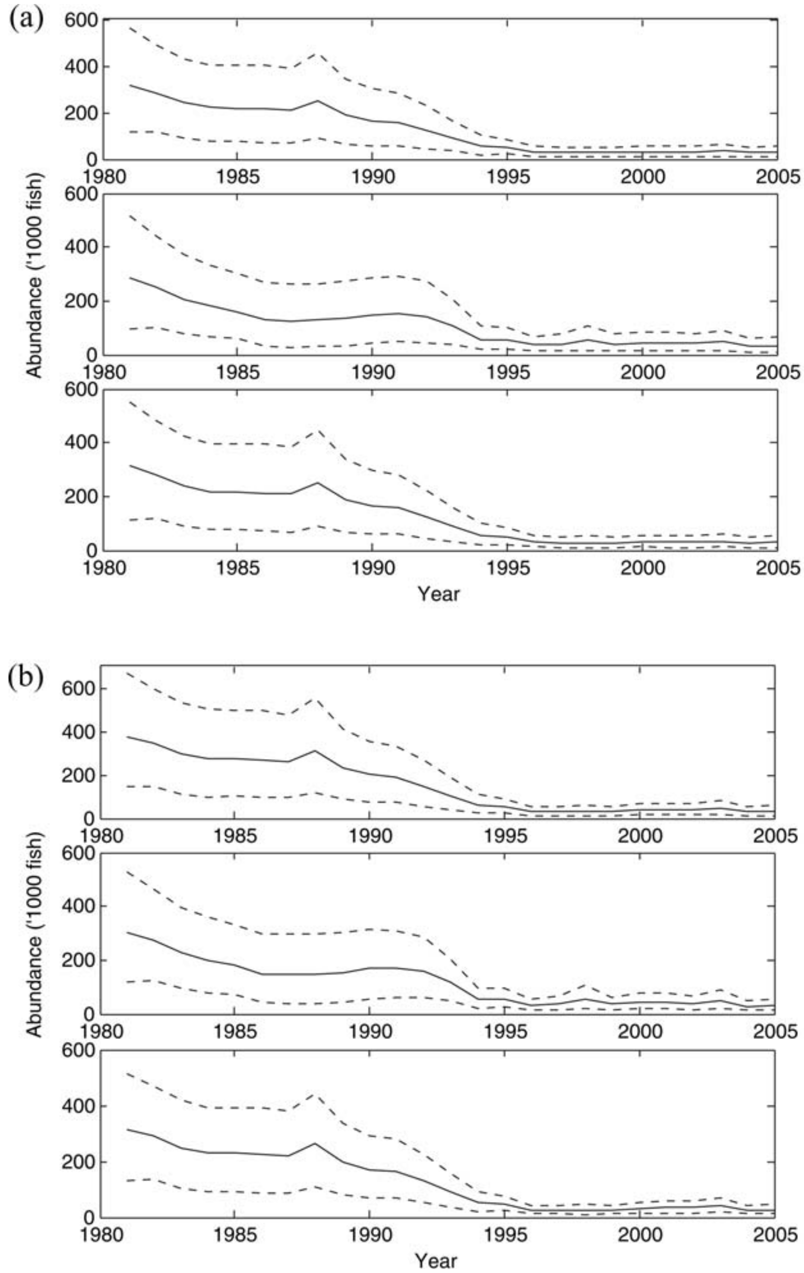

Figure 4. Population abundance trajectories (in thousands of individuals) from (a) the state-space surplus production model with a multilevel prior of population growth rate, and (b) the time-varying hierarchical state-space surplus production model. Shown from top to bottom in each multi-panel are the results for scenarios S1, S2, and S3. Continuous lines over years denote the mean, and dotted lines the 95% probability intervals of population abundance.

model, $\bar{D}$ the posterior mean of the deviance, and $\hat{D}$ the deviance of the posterior mean. The DIC is a hierarchical modelling generalization of the Akaike information criterion (AIC) and the Bayesian information criterion (BIC, also known as the Schwarz criterion). It is particularly useful in Bayesian model selection problems, where the posterior distributions of the models have been obtained by MCMC simulation. Like AIC and BIC, it is an asymptotic approximation as the sample size becomes large. It is only valid when the posterior distribution is approximately multivariate normal (Spiegelhalter *et al.*, 2002, 2004).

Results

Use of a hierarchically structured model generally resulted in parameter estimates with a wider credible interval than using a non-hierarchical model (Table 1). The credible intervals of r, K, and N_{1981} were considerably wider when the hierarchical model was used than with the non-hierarchical state-space surplus production model.

Using a lognormal error structure generally resulted in smaller DIC values than a gamma error structure (Table 2), so we present results for models with lognormal error structures for both process and observation errors. Compared with the non-hierarchical state-space surplus production model, the hierarchical approaches used here fitted the data considerably better. The DIC values were ~27–36 for the models with a multilevel prior of population growth rate, compared with ~43–45 for the non-hierarchical models (Table 2). The DIC values were ~14–19 for the time-varying hierarchical models, compared with ~43–45 for the non-hierarchical models (Table 2). DIC values and parameter estimates were also influenced by the choice of priors (Tables 1 and 2).

Results from scenarios 1 and 3 showed that the posteriors of r, K, and N_{1981} were stable when the multilevel prior of r was used and when the variance of the hyperparameters was increased by a factor of 5, whereas results from the non-hierarchical model were more sensitive to changes in the priors (Table 1). The posterior distribution of $\bar{r}$ changed substantially when the variance of the hyperprior was expanded, which is predictable because the distribution of $\bar{r}$ was strongly influenced by the hyperpriors, the mean and variance of $\bar{r}$. The results from scenarios 1 and 2 showed that the posteriors of r, K, and N_{1981} were stable when the multilevel prior of r and the PLL or PLLOP index were used, whereas results from the non-hierarchical model were more sensitive to the catch-rate index (Table 1).

Results from the Bayesian state-space surplus production model with the multilevel prior of r were therefore rather consistent across the scenarios considered (Table 1, Figures 3, 4a, and 5a). The posterior distribution of $\bar{r}$ followed a wide normal distribution, implying a wide range of population growth rates among species. The population growth rate, r, was slightly lower in scenario 1 (median = 0.30) than in scenarios 2 and 3 (mean = 0.31 or 0.32; Table 1, Figure 3). Population abundance in 1981, N_{1981}, was smaller in scenario 2 than in scenarios 1 and 3, and population abundances after 1990 were higher in scenario 2 than in scenarios 1 and 3. Depletion estimated in scenario 2 was larger than in scenarios 1 and 3. In general, the differences in estimated parameters among scenarios were not large.

Results from the time-varying Bayesian hierarchical state-space surplus production model were fairly consistent across the

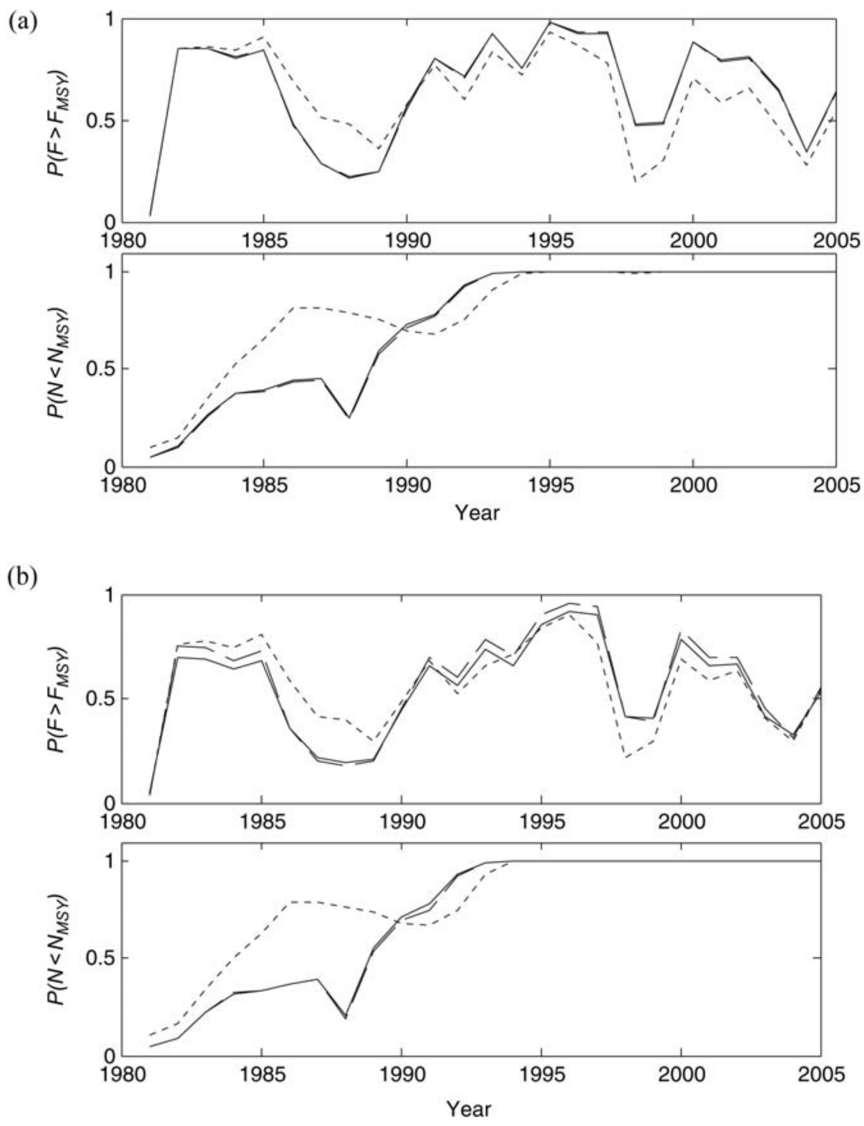

Figure 5. The probability of fishing mortality being larger than F_{MSY} and of population size being smaller than N_{MSY} from (a) the hierarchical state-space surplus production model with a multilevel prior of population growth rate, and (b) the time-varying hierarchical state-space surplus production model. Solid line, scenario S1; dotted line, S2; dashed line, S3.

scenarios considered (Figures 4b, 5b, and 6). The posterior distribution of $\bar{r}$ followed a wide normal distribution, implying a wide range of population growth rates among species. The population growth rate, r_t, showed more variation after the mid-1990s, with mean values fluctuating between 0.10 and 0.40 (Figure 6).

The Bayesian state-space surplus production models with the multilevel prior of r and the time-varying Bayesian hierarchical state-space surplus production model both fitted the data well (Figure 7a and b). The fit was influenced more by the PLL and PLLOP relative abundance series than by the shorter NMFS-SE and BLLOP series.

The population abundance estimates from the three scenarios in the two hierarchically structured models showed that population size has decreased since 1981, especially after 1990. Abundance was relatively stable after 1995, when mean values were in the range 25 000–30 000 sharks in scenarios 1 and 3, and 35 000–45 000 sharks in scenario 2 (Figure 4). Both hierarchically structured models showed similar results. There was an increase in abundance from 1989 to 1993 in scenario 2 that made the overall population trajectory pattern different from those in scenarios 1 and 3, which increase in 1988. These results were probably driven by the PLL time-series in 1988, which showed a marked peak. In contrast, scenario 2 used the PLLOP time-series, which resulted in a smoother trajectory of population size around 1988 (the first year of relative abundance data was 1992 in this scenario).

The population became overfished after 1993 and overfishing occurred from 1982 to 1985 and from 1991 to 1997; the risk of overfishing was intermediate in recent years (between 55 and 65%; Figure 5a and b). Both hierarchically structured models showed similar results.

Discussion

In this study, the hierarchical Bayesian models (with a multilevel prior of r or with a time-varying r through a hierarchical prior) consistently fitted the hammerhead complex data better than the non-hierarchical models, a statement supported by the results of the sensitivity analyses. This suggests that a hierarchical Bayesian model or the use of multilevel priors is mathematically viable and valuable in modelling the hammerhead complex and potentially other fish complexes. However, this study also revealed that informative priors influence the results of both model parameters and DIC values. The use of informative priors and model choice may also need to be justified based on an understanding of the biology of each species or complex. Here, both the model goodness-of-fit and the fact that the ability to incorporate the growth-rate variation among species in the complex suggest that the hierarchical state-space surplus production model is a better choice.

Multilevel priors are robust priors because of the stability of model results (Roberts and Rosenthal, 2001). Our study has shown consistent results across three scenarios with a multilevel prior. Compared with the commonly used priors, multilevel priors may therefore be better choices as robust priors. The number of levels of priors will depend on the parameters of interest. For example, here we were interested in the population growth rate

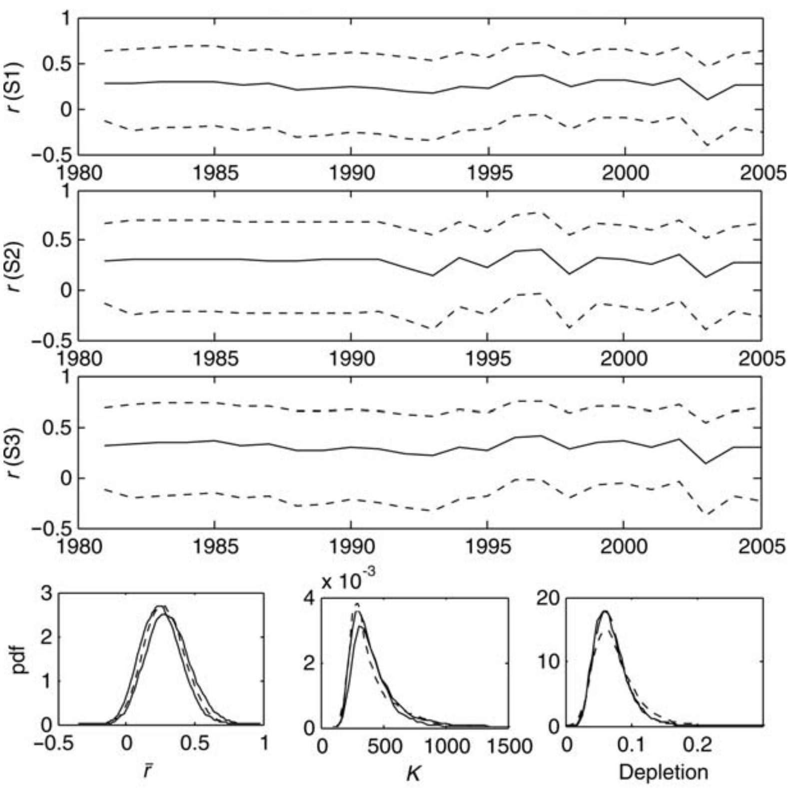

Figure 6. Estimates of the time-varying population growth rate and probability density functions (pdf) of key parameters from the time-varying hierarchical state-space surplus production model (continuous lines over years denote the mean, and dotted lines 95% probability interval). Solid line, scenario S1; dotted line, S2; dashed line, S3. K is in thousands of individuals.

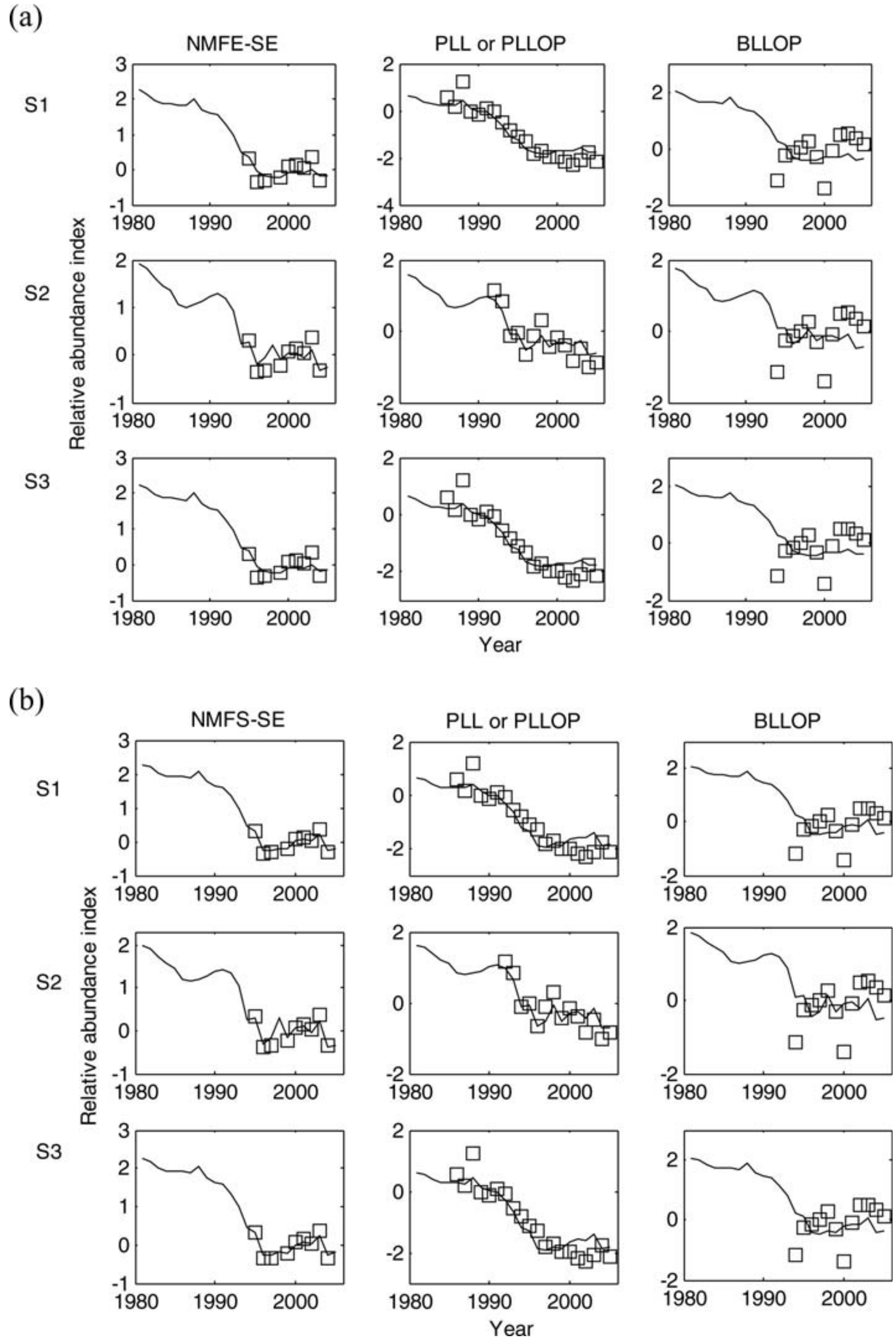

Figure 7. Model fits to catch-rate data from (a) the hierarchical state-space surplus production model with a multilevel prior of population growth rate, and (b) the time-varying hierarchical state-space surplus production model.

r rather than the hyperparameter $\bar{r}$, so we had two levels of hyperparameter, which resulted in a stable distribution of *r*.

Our results suggest that the status of the hammerhead shark complex along the US Atlantic and Gulf of Mexico coasts is as found by Baum *et al*. (2003), but not as depleted as found by Myers *et al*. (2007). However, our study was based on a complex, and current stock status (for 2005) is still overfished, and the probability of overfishing occurring is still considerable. Our results can be used to formulate further hypotheses about the status of the complex, which need to be tested by gathering more empirical data. The study also suggests that it may be necessary to decrease fishing mortality to decrease the risk of overfishing ($P(F > F_{\mathrm{MSY}})$). A proposed quota reduction for all large coastal sharks in US waters would undoubtedly help hammerhead stocks to rebuild more quickly (NMFS, 2006).

Although there have been few studies on the biology of great and smooth hammerheads, it is likely that the two species have population growth rates that differ substantially from those of scalloped hammerheads (EC, unpublished data). Even intraspecifically, variability among populations may well exist because of different habitat or other environmental conditions (Clark, 2003). Because the species in the complex likely have different population growth rates, the average growth rate of the complex may vary over time as a result of varying fishing pressure on the individual species. Species with fast population growth rates are therefore likely exposed to less exploitation risk than their counterparts with slower population growth rates under the current management strategy. These are reasons that motivate the use of hierarchical modelling.

There is evidence that even intraspecific population growth rate can vary over time as a consequence of climate variation, for example (Beamish *et al*., 1999; Peterman *et al*., 2003), and that population growth rate tends to be autocorrelated over time (Halley and Kunin, 1999; Morales, 1999; Schwager *et al*., 2006). The hierarchical time-varying population growth model can simulate population growth rate variation caused by the hierarchy of growth rates, which has been related to regime shifts, and changes in productivity regimes (Beamish *et al*., 1999; Clark, 2003). Models such as the residual autoregressive model (where residuals of the exponential growth model are assumed to be autocorrelated; Morales, 1999; Schwager *et al*., 2006), the population growth autoregressive model (population growth rates are assumed to be autocorrelated to simulate the coloured environmental noise; Morales, 1999; Schwager *et al*., 2006), and the population growth random-walk model (a special case of the auto-regressive model with fewer parameters; Peterman *et al*., 2003) may be considered in future.

The reasons for the discrepancy in relative abundance trends between the pelagic and bottom longline fisheries and the NMFS-SE survey data are not immediately apparent. Possible reasons could be that the bottom longline fishery observer programme was only voluntary until 2001 and that the NMFS-SE survey, although fishery-independent, has a small sample size.

The Bayesian hierarchical approach demonstrated here represents an intermediate strategy between traditional models that does not allow for variability in the productivity of different species or species complexes and highly parameterized models that assign an estimate to each species. Hierarchical models are more flexible than non-hierarchical methods, because they allow one to consider variation in the modelling objective that can be caused by natural variation between different species, in fishing pressure, and in environmental changes (Gelfand and Smith, 1990; Zeger and Karim, 1991; Clark, 2003).

Non-hierarchical models treat population growth rates as fixed constants, and it is difficult to allow for variability (Clark, 2003). By ignoring variability among species, confidence intervals of the estimates can be unrealistically narrow, possibly leading to adoption of high-risk management strategies. A hierarchical Bayesian approach is instead recommended when modelling fish complexes, as applied here. The approach improves the model goodness-of-fit, allows incorporation of variability among species, and generally provides better inferences.

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