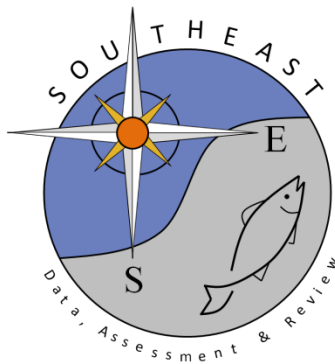


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Yan Jiao, Enric Corte's, Kate Andrews, And Feng Guo

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Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach

YAN JIAO,^{1,4} ENRIC CORTÉS,² KATE ANDREWS,² AND FENG GUO³

¹Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061-0321 USA

²National Marine Fisheries Service, Panama City Laboratory, Panama City, Florida 32408 USA

³Department of Statistics, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0439 USA

Abstract. Appropriate inference for stocks or species with low-quality data (poor data) or limited data (data poor) is extremely important. Hierarchical Bayesian methods are especially applicable to small-area, small-sample-size estimation problems because they allow poor-data species to borrow strength from species with good-quality data. We used a hammerhead shark complex as an example to investigate the advantages of using hierarchical Bayesian models in assessing the status of poor-data and data-poor exploited species. The hammerhead shark complex (*Sphyrna* spp.) along the Atlantic and Gulf of Mexico coasts of the United States is composed of three species: the scalloped hammerhead (*S. lewini*), the great hammerhead (*S. mokarran*), and the smooth hammerhead (*S. zygaena*) sharks. The scalloped hammerhead comprises 70–80% of the catch and has catch and relative abundance data of good quality, whereas great and smooth hammerheads have relative abundance indices that are both limited and of low quality presumably because of low stock density and limited sampling. Four hierarchical Bayesian state-space surplus production models were developed to simulate variability in population growth rates, carrying capacity, and catchability of the species. The results from the hierarchical Bayesian models were considerably more robust than those of the nonhierarchical models. The hierarchical Bayesian approach represents an intermediate strategy between traditional models that assume different population parameters for each species and those that assume all species share identical parameters. Use of the hierarchical Bayesian approach is suggested for future hammerhead shark stock assessments and for modeling fish complexes with species-specific data, because the poor-data species can borrow strength from the species with good data, making the estimation more stable and robust.

Key words: Bayesian hierarchical model; data-poor assessment; hammerhead shark; fish complex; population dynamics; small sample size.

INTRODUCTION

It is widely recognized by analysts that population assessments of species that have poor data (where quality is poor) or are data poor (where data are limited in quantity) are very challenging. Because of this dual limitation, assessments of the status of exploited populations are often highly uncertain. Assessments of poor-data and data-poor species are thus often based on life history information (e.g., matrix models and per-recruit analysis; Mace and Sissenwine 1993, Fujiwara and Caswell 2001, Cortés 2002a) or abundance indices or catch histories (e.g., an index method; NEFSC 2008a, MacCall 2009, Northeast Data Poor Stocks Working Group 2009). Methods that can generally improve the reliability of stock assessments in poor-data and data-poor situations are thus urgently needed.

Hierarchical Bayesian methods are especially applicable to small-area and small-sample-size estimation problems because they allow poor-data species to borrow strength from species with good-quality data (Berger 1985, He and Sun 1998, 2000, Su et al. 2001, Gelman et al. 2004). Many hierarchical modeling analyses based on empirical data and simulations reveal the need for multilevel analysis of multilevel data (He and Sun 2000, Osborne 2000, Su et al. 2001). Hierarchical and multilevel models are the same in concept but different terminology is used according to the discipline. Additionally, hierarchical modeling analyses provide other benefits, such as easy modeling of cross-level interactions. This often allows for more interesting questions to be asked of the data, such as estimating parameters or variables of interest across experiments, locations, and times (Osborne 2000). With nested and hierarchical data being common in the social and other sciences, recent developments in Bayesian approaches, and the availability of high-performance computers that make hierarchical models solvable and

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⁴ E-mail: yjiao@vt.edu

accessible, it is important for fisheries researchers to become more acquainted with the application of Bayesian hierarchical techniques to assess the status of data-poor and poor-data species.

In this study, we used a hammerhead shark complex as an example to demonstrate the advantages of using hierarchical Bayesian models in assessing the status of poor-data and data-poor species. The hammerhead shark complex (*Sphyrna* spp.) along the Atlantic and Gulf of Mexico coasts of the USA is composed of three species: the scalloped hammerhead (*S. lewini*), the great hammerhead (*S. mokarran*), and the smooth hammerhead (*S. zygaena*) sharks. Stock assessments of sharks often have had to focus on complexes, such as the large and small coastal sharks in the USA, because of the lack of species-specific data (Cortés 2002b, NMFS 2006). It is common to find that there are species with good data available and other species with only poor data in a fish complex (NMFS 2006, NEFSC 2008a, b). This is also true for other fisheries, such as those for the snapper-grouper complex in the U.S. South Atlantic and Gulf of Mexico and some ground fishes in the U.S. North Atlantic (Polovina and Ralston 1987). The approach of hierarchical modeling for fish complexes used by Jiao et al. (2009a) was recently endorsed by the U.S. National Research Council and by a recent independent review for NOAA of the Hawaiian bottomfish fishery (NMFS 2009, NRC 2010). We further developed this study to deal with data-poor species in fish complexes.

In the examples used here, great and smooth hammerheads have relative abundance data that are both limited in quantity and of low quality, presumably because of low population densities and limited sampling (Hayes 2008). However, within the complex, the scalloped hammerhead shark comprises 70–80% of the catch and several series of relative abundance of fairly high quality are available, in contrast to the data for great and smooth hammerhead sharks. The three species are distributed in the same geographical areas and are exploited by the same fisheries. Because of the relatively low density of these sharks in the ocean and because of the limited efforts allocated to collecting data from both fishery-dependent and fishery-independent sources, the status of great and smooth hammerheads is largely unknown and the paucity of data led to inconclusive results (IUCN 2006, Hayes 2008). This situation, with one species having data of good quality and two species having limited, low-quality data, provides a good example to illustrate how hierarchical Bayesian models can improve assessment of the species with poor data by allowing them to borrow strength from the species with good-quality data (He and Sun 1998, Su et al. 2001, Gelman et al. 2004).

Population dynamics models that have been used for shark complexes are based on surplus production theory (see, e.g., NMFS 2006). In this study, variability among species is modeled with a hierarchical approach to address the problem of simulating population growth

rates assigned to a particular species. In contrast to an overfitted model that would assign a different parameter value to each species, hierarchical models accommodate species or group differences but assume these differences are derived from an underlying distribution through hierarchical prior distributions (Wikle 2003, Gelman et al. 2004).

The hierarchical model was implemented in a Bayesian framework. Bayesian approaches commonly have been used in solving hierarchical models because of their flexibility in incorporating multiple levels of randomness and information from different sources. They are increasingly being used in fisheries stock assessment because of their ability to provide results for risk analyses of alternative management strategies and to incorporate prior knowledge of the fisheries into the assessment process (Berger 1985, McAllister and Kirkwood 1998, Gelman et al. 2004). Hierarchical Bayesian models have also shown robustness to prior specification and data uncertainty (Roberts and Rosenthal 2001).

Demographic data help us understand the basis of population dynamics and are especially useful when the populations are too sparse to assess (Kieth and Windberg 1978, Krebs et al. 2001). Population growth rate estimates based on demographic information can be used as prior knowledge in a hierarchical framework and help us to better simulate the population dynamics (Jiao et al. 2008, 2009a). In this example, demographic information of hammerhead sharks and other shark species is synthesized and used as prior information (Jiao et al. 2009a).

The goodness of fits of the Bayesian hierarchically structured surplus production models were compared with that of the traditional nonhierarchical surplus production model for each species using the deviance information criterion (DIC; Spiegelhalter et al. 2004). Robustness of the model fit was also used to compare models (Roberts and Rosenthal 2001). Our ultimate goal was to evaluate the Bayesian hierarchical model as an appropriate method to assess the population dynamics of data-poor and poor-data species. The framework developed here can be used to assess other species with similar data shortcomings.

METHODS

Data sources

Data on hammerhead sharks were collected and summarized from several National Marine Fisheries Service (NMFS) sources (Beerkircher et al. 2002, Cortés et al. 2005, Cortés and Neer 2005, NMFS 2006, Hayes 2008; see Plate 1). Catch time series included recreational catches, commercial landings, and pelagic longline discards (Fig. 1). Relative abundance time series included the NMFS Mississippi bottom-longline shark survey (NMFS-LL-SE, in number of sharks per 10 000 hook hours; Ingram et al. 2005), the NMFS Panama City gillnet shark survey (PCGN, in number of sharks per net per hour; Carlson and Bethea

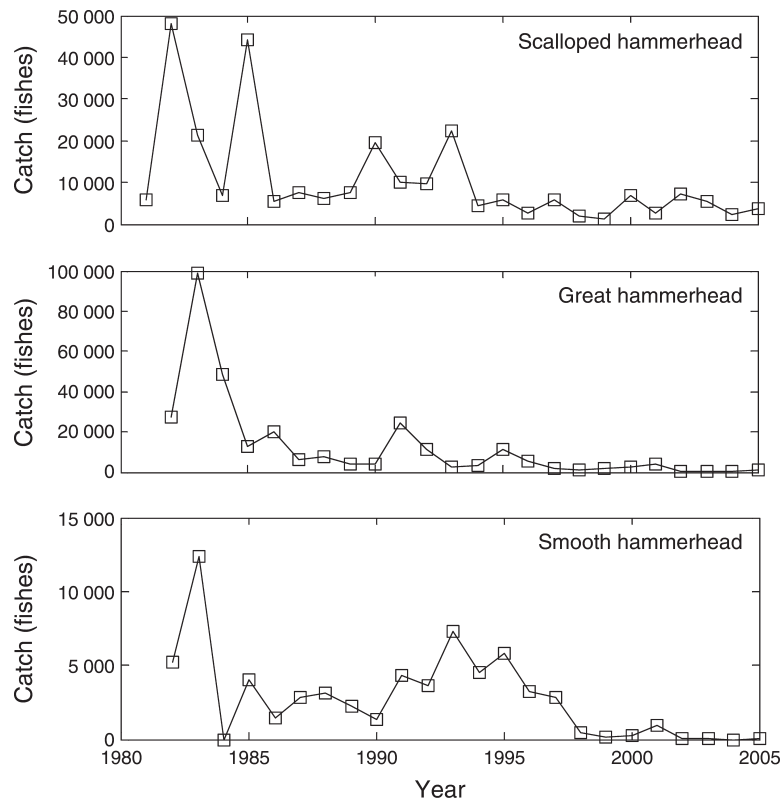


FIG. 1. Summarized catches (in numbers) of hammerhead sharks by species.

2005), the University of North Carolina longline survey (NCLL, in number of sharks per hook; Schwartz et al. 2007), the commercial shark fishery observer program (CSFOP, in number of sharks per 100 hooks per hour; Cortés et al. 2005), the shark drift gillnet observer program (GNOP in number of sharks per 10^7 m² per hour; Carlson et al. 2005), and the pelagic longline observer program (PLLOP, in number of sharks per 1000 hooks; Beerkircher et al. 2002; Fig. 2). Not all series have catch-per-unit-effort (CPUE) information for each species. Six series (NMFS-LL-SE, PCGN, NCLL, CSFOP, GNOP, and PLLOP) were available for scalloped hammerhead sharks because of the high portion of the hammerhead shark complex catch that this species represents, but only two relative abundance indices were available for great hammerhead (NMFS-LL-SE and CSFOP) and one for smooth hammerhead sharks (PLLOP).

To compare the Bayesian hierarchically structured surplus production model to the traditional nonhierarchical surplus production model for each species, we first described the nonhierarchical surplus production model, followed by the hierarchical surplus production model with species-specific data. We named the nonhierarchical model M1. This model (M1) consisted of three models with the same structure, but was fitted to three different species, i.e., one model for each species. Four hierarchical models were developed in this study: the first model

had population growth rate hierarchically structured (M2); the second one had population growth rate and carrying capacity hierarchically structured (M3); the third one set population growth rate and catchability to be hierarchically structured (M4); whereas the fifth one (M5) set population growth rate, carrying capacity and catchability all to be hierarchically structured.

Bayesian state-space surplus production model for each species

Because the data available on hammerhead sharks were not size, age, or stage structured and process error is often very important, we used a state-space surplus production model as the basic model structure (M1):

$$E(N_{k,t}) = N_{k,t-1} + G_{k,t-1} - C_{k,t-1}$$

$$E(I_{i,k,t}) = q_{i,k}N_{k,t} \quad (1)$$

where k indicates the species (here $k = 1$ means scalloped hammerhead shark, $k = 2$ means great hammerhead shark, and $k = 3$ means smooth hammerhead shark); i is the i th type of relative abundance index (here i ranges from 1 to 6 and represents relative abundance indices from surveys of NMFS-LL-SE, PCGN, NCLL, CSFOP, GNOP, and PLLOP, separately); $N_{k,t}$ is the abundance (in 1000 sharks) of species k in year t ; $G_{k,t}$ is the production function of species k in year t ; $C_{k,t}$ is the total catch (in 1000 sharks) of species k in year t ; and $q_{i,k}$

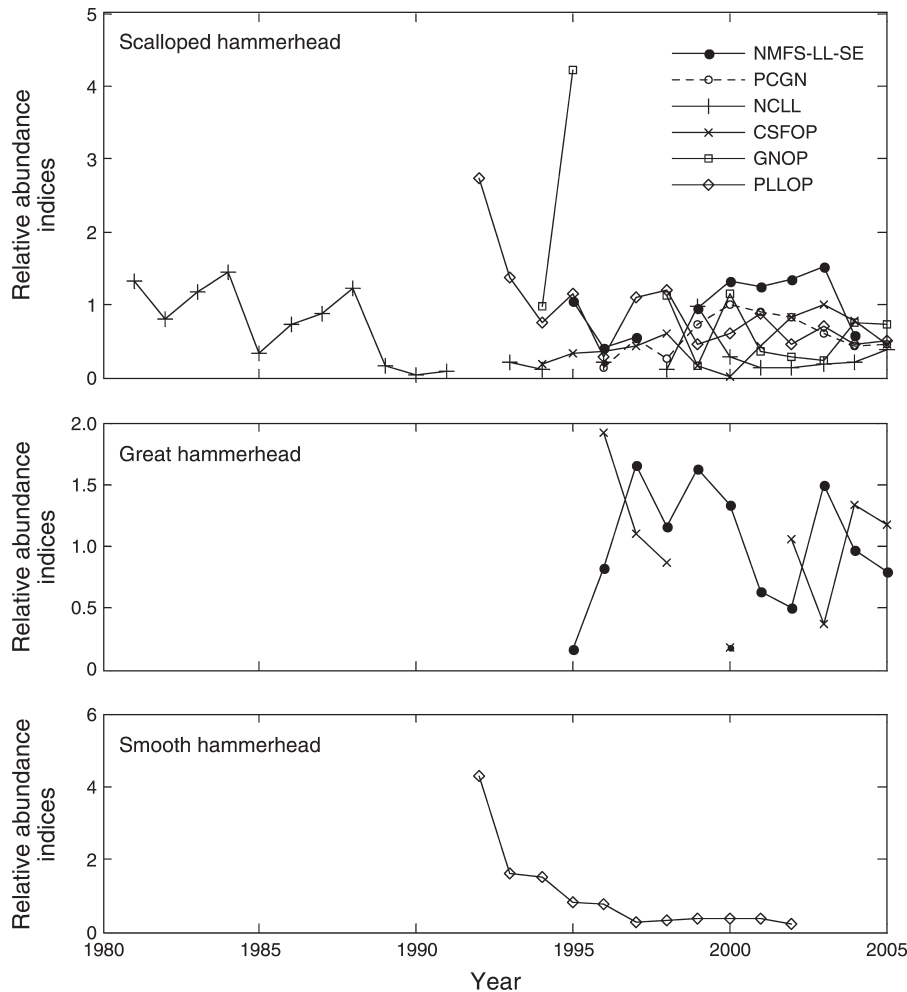


FIG. 2. Indices of relative abundance for hammerhead sharks by species. See *Methods: Data sources* for a description of the acronyms in the legend and the units.

is the catchability coefficient for the i th type of relative abundance index $I_{i,k}$ of species k . Because the units of $I_{i,k}$ are different (see Data Sources), the units of $q_{i,k}$ are different for different i . The unit of $I_{1,k}$ is per 10 million hook hour; the unit of $I_{2,k}$ is per thousand net per hour; the unit of $I_{3,k}$ is per thousand hooks; the unit of $I_{4,k}$ is per 100 thousand hooks per hour; the unit of $I_{5,k}$ is per 10 billion m^2 per hour; and the unit of $I_{6,k}$ is per million hooks. Here we used the Schaefer model, $G_{k,t} = r_k N_{k,t} (1 - N_{k,t} / K_k)$, as the production function, which is widely used in fisheries and ecology (May et al. 1979, Hilborn and Walters 1992), where r_k is the population growth rate of species k and K_k is the carrying capacity of species k . Parameter r_k was assumed to follow a normal distribution with mean $a_1 = 0.0661$ and variance $a_2 = 0.0996$. The values 0.0661 and 0.0996 are based on summarized information on the population growth rate of 80 shark species and stocks (Hoenig and Gruber 1990, Cailliet et al. 1992, Sminkey and Musick 1995, Smith et al. 1998, Cortés 2002a, Mollet and Cailliet

2002). The carrying capacity of each species, K_k , was assumed to follow a uniform distribution (U) with lower bound $K_{\min,k}$ and upper bound $K_{\max,k}$. Maximum observed catch of species k was used as the value of $K_{\min,k}$. The upper bound K_{\max} was assumed to be the estimated carrying capacity of large coastal sharks (35 677 000 sharks; NMFS 2006). The prior for N_{1981} , the abundance in the first year of our model, followed a lognormal distribution. We further assigned a uniform distribution between 1% and 100% of K for the median of the prior for N_{1981} . The sensitivities of model results to these priors were explored (see *Sensitivity analysis* and Table 1).

The hierarchical Bayesian surplus production model with species-specific data

When the species-specific data were treated as hierarchically structured, instead of assessing each species separately, the three species were assessed together through a Bayesian hierarchical model. In the

TABLE 1. Prior specification in seven scenarios used in sensitivity analyses.

Scenarios and models	Priors in the models
S1	
M1	$r \sim \mathcal{N}(0.061, 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677)$; $q_{i,k} \sim U(0.0001, 3)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.00001, 1)$
M2	$\bar{r} \sim \mathcal{N}(0.061, 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677)$; $CV_i \sim U(20\%, 40\%)$; $q_{i,k} \sim U(0.0001, 3)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.00001, 1)$
M3	$\bar{r} \sim \mathcal{N}(0.061, 0.0996)$; $\bar{K}_{\max} \sim U(\max[\text{catch}], 35677)$; $CV_i \sim U(20\%, 40\%)$; $q_{i,k} \sim U(0.0001, 3)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.00001, 1)$
M4	$\bar{r} \sim \mathcal{N}(0.061, 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677)$; $CV_i \sim U(20\%, 40\%)$; $\bar{q}_{i,k} \sim U(0.0001, 3)$; $q_{i=2,3,5,k=1}$
M5	$\bar{r} \sim \mathcal{N}(0.061, 0.0996)$; $\bar{K}_{\max} \sim U(\max[\text{catch}], 35677)$; $CV_i \sim U(20\%, 40\%)$; $\bar{q}_{i,k} \sim U(0.0001, 3)$; $q_{i=2,3,5,k=1}$
S2	
M1	$r \sim \mathcal{N}(0.061, 5 \times 0.0996)$; others same as S1
M2	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; others same as S1
M3	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; others same as S1
M4	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; others same as S1
M5	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; others same as S1
S3	
M1	$r \sim U(-0.2, 1)$; others same as S1
M2	$\bar{r} \sim U(-0.2, 1)$; others same as S1
M3	$\bar{r} \sim U(-0.2, 1)$; others same as S1
M4	$\bar{r} \sim U(-0.2, 1)$; others same as S1
M5	$\bar{r} \sim U(-0.2, 1)$; others same as S1
S4	
M1	$K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M2	$K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M3	$\bar{K}_k \sim U(\max[\text{catch}], 35677 \times 10)$; others same as S1
M4	$K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M5	$\bar{K}_k \sim U(\max[\text{catch}], 35677 \times 10)$; others same as S1
S5	
M1	$r \sim \mathcal{N}(0.061, 5 \times 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M2	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M3	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; $\bar{K}_{\max} \sim U(\max[\text{catch}], 35677 \times 10)$; others same as S1
M4	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; $K_k \sim U(\max[\text{catch}_k], 35677 \times 10)$; others same as S1
M5	$\bar{r} \sim \mathcal{N}(0.061, 5 \times 0.0996)$; $\bar{K}_{\max} \sim U(\max[\text{catch}], 35677 \times 10)$; others same as S1
S6	
M1	$\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.000001, 2)$; others same as S1
M2	$CV_i \sim U(10\%, 60\%)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.000001, 2)$; others same as S1
M3	$CV_i \sim U(10\%, 60\%)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.000001, 2)$; others same as S1
M4	$CV_i \sim U(10\%, 60\%)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.000001, 2)$; others same as S1
M5	$CV_i \sim U(10\%, 60\%)$; $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2 \sim U(0.000001, 2)$; others same as S1
S7	
M1	$q_{i,k} \sim U(0.00001, 10)$; others same as S1
M2	$q_{i,k} \sim U(0.00001, 10)$; others same as S1
M3	$q_{i,k} \sim U(0.00001, 10)$; others same as S1
M4	$\bar{q}_{i,k} \sim U(0.00001, 10)$; $q_{i=2,3,5,k=1} \sim U(0.00001, 10)$; others same as S1
M5	$\bar{q}_{i,k} \sim U(0.00001, 10)$; $q_{i=2,3,5,k=1} \sim U(0.00001, 10)$; others same as S1

Notes: Each scenario included five models: M1, nonhierarchical priors; M2, hierarchical prior of growth rate, r ; M3, hierarchical priors of r and carrying capacity, K ; M4, hierarchical priors of r and catchability coefficient, q ; M5, hierarchical priors of r , K , and q . K values are in thousands. The subscript k indicates the species; i is the i th type of relative abundance index, I ; N is the abundance. $U(\max[\text{catch}])$ is the uniform distribution of the maximum observed catch.

first hierarchical model, only r was modeled to be hierarchically structured (M2)

$$G_{k,t} = r_k N_{k,t} (1 - N_{k,t}/K_k)$$

$$r_k \sim \mathcal{N}(\bar{r}, [\text{CV}_1 \times \bar{r}]^2)$$

$$\bar{r} \sim \mathcal{N}(a_1, a_2)$$

$$\text{CV}_1 \sim U(b_1, b_2)$$

$$K_k \sim U(K_{\min,k}, K_{\max}). \quad (2)$$

Model M2 was used to simulate possible differences of the population growth rates of the three species in the complex via a hierarchical specification. The intrinsic rate of population growth, r_k , was assumed to follow a normal distribution with mean \bar{r} and variance $(\text{CV}_1 \times \bar{r})^2$. However, mean \bar{r} and coefficient of variation CV_1 are hyperparameters. The parameter \bar{r} itself was assumed to follow a normal distribution with mean $a_1 = 0.0661$ and variance $a_2 = 0.0996$. The carrying capacity of each species, K_k , was assumed to follow a uniform distribution with lower bound $K_{\min,k}$ and upper bound K_{\max} . Maximum observed catch of species k was used as the value of $K_{\min,k}$. However, the upper bound K_{\max} is

the estimated carrying capacity of large coastal sharks (35 677 000 sharks; NMFS 2006). Sensitivity of model results to these values and the hierarchical structure of r was explored (see *Sensitivity analysis*). Values of CV of 20–40% have been treated as a reasonable range for fisheries data (Walters 1998); thus in the base scenario (S1), CV_1 and CV_2 were assumed to range between 20% and 40%. We nevertheless tested the sensitivity of this assumption by extending the range to 10–60% in the sensitivity analysis.

In the second hierarchical model, both r and K were assumed to be with hierarchically structured priors (M3)

$$\begin{aligned} G_{k,t} &= r_k N_{k,t} (1 - N_{k,t}/K_k) \\ r_k &\sim \mathcal{N}(\bar{r}, [CV_1 \times \bar{r}]^2) \\ \bar{r} &\sim \mathcal{N}(a_1, a_2) \\ CV_1 &\sim U(b_1, b_2) \\ K_k &\sim U(K_{\min,k}, K_{\max,k}) \\ K_{\max,k} &\sim \mathcal{N}(\bar{K}_{\max}, [CV_2 \times \bar{K}_{\max}]^2) \\ \bar{K}_{\max} &\sim U(c_1, c_2) \\ CV_2 &\sim U(d_1, d_2). \end{aligned} \quad (3)$$

In this model, the carrying capacity of each species, K_k , was assumed to follow a uniform distribution with lower bound $K_{\min,k}$ and upper bound $K_{\max,k}$. Maximum observed catch of species k was used as the value of $K_{\min,k}$. However, the upper bound $K_{\max,k}$ itself followed a two-level distribution with mean \bar{K}_{\max} , and variance, $(CV_2 \times \bar{K}_{\max})^2$. The parameter \bar{K}_{\max} was assumed to follow a uniform distribution with lower bound c_1 , the maximum observed catch of large coastal sharks (1 200 000 sharks) and upper bound, c_2 , the estimated carrying capacity of large coastal sharks (35 677 000 sharks; NMFS 2006). The use of $K_{\max,k} \sim \mathcal{N}(\bar{K}_{\max}, [CV_2 \times \bar{K}_{\max}]^2)$ incorporated uncertainty in the estimated carrying capacity of large coastal sharks into the prior information, compared with using an arbitrarily inflated prior for K_{\max} . Sensitivity of model results to these values and the hierarchical structure of r , K , CV_1 , and CV_2 were explored (see *Sensitivity analysis*).

The surveys for relative abundance indices for great and smooth hammerheads were also available for scalloped hammerheads. In the fourth model (M4), both r and $q_{i,k}$ was hierarchically structured to incorporate the potential similarity and relationship among catchability of the species ($q_{i,k}$) if they appear in the same survey. According to the surveys and the species available in each survey, we can write the distributions of $q_{i,k}$ as follows:

$$\begin{aligned} q_{i=1,4,k=1,2} &\sim \mathcal{N}(\bar{q}_i, [\bar{q}_i \times CV_3]^2) \\ q_{i=6,k=1,3} &\sim \mathcal{N}(\bar{q}_i, [\bar{q}_i \times CV_3]^2) \\ q_{i=2,3,5,k=1} &\sim U(c_{i,1}, c_{i,2}) \\ \bar{q}_i &\sim U(c_{i,1}, c_{i,2}) \\ CV_3 &\sim U(e_1, e_2), \end{aligned} \quad (4)$$

where $c_{i,1}$ and $c_{i,2}$, the lower and upper bounds of \bar{q}_i , are assumed to be 0.0001 and 3; CV_3 is the CV of $q_{i,k}$ and is assumed to vary between 20–40% (i.e., limit $e_1 = 20\%$, $e_2 = 40\%$). It also implied that for surveys in which only one species was observed (i.e., $i = 2, 3, 5$), a nonhierarchical model was used, i.e., $q_{i=2,3,5,k=1}$ follows a uniform distribution with lower and upper bounds $c_{i,1}$ and $c_{i,2}$. Sensitivities to these prior values were tested (see *Sensitivity analysis*).

We also developed a model to allow r , K , and q to be all hierarchically structured (M5), i.e., a hybrid of M3 and M4. Priors used in M3 and M4 were used in this model also. Sensitivities to these prior values were tested.

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, was used in this study (Millar and Meyer 2000, de Valpine and Hastings 2002). Process error associated with the production and population dynamics equations is critically important given the simplicity of the production equation and potentially chaotic environmental changes. Recent research on comparison of the observation-error estimator and the observation-process-error estimator also suggests the importance of using the observation-process-error estimator (de Valpine and Hastings 2002, Calder et al. 2003).

A lognormal error structure was used for both the process and observation errors, i.e., the log-transformed population abundance $\ln(N_{k,t})$ followed a normal distribution with mean $\ln(N_{k,t-1} + G_{k,t-1} - C_{k,t-1})$ and variance $\sigma_{k,N}^2$; the log-transformed relative population abundance $\ln(I_{i,k,t})$ followed a normal distribution with mean $\ln(q_{i,k} N_{k,t})$ and variance $\sigma_{i,k,I}^2$. Priors for $\sigma_{k,N}^2$ and $\sigma_{i,k,I}^2$ were assumed to be uniform distributions between 0.00001 and 1. To test the influence of these priors, $U(0.000001, 2)$ was used in a sensitivity analysis.

Bayesian approach and priors

Presently only Bayesian methods are computationally possible for a hierarchically structured process-observation error model, and the traditional maximum likelihood methods cannot solve it unless some assumptions are made for the process error (de Valpine and Hastings 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, Gelman et al. 2004). The Bayesian approach was used to estimate both the uncertainty in parameter estimates and population abundance. A nonhierarchical Bayesian model for each species specifies a posterior density for parameters ($p(\theta|I)$) using Bayes’ theorem. When species k is considered, the posterior probability of all the parameters, represented by θ_k , given observation of I_k can be written as

$$p_k(\theta_k|I_k) \propto L(I_k|N_k, q_k, \sigma_{k,I})\pi(N_k|r_k, K_k, \sigma_{k,N}) \times \pi(q_k, \sigma_{k,I})\pi(r_k, K_k, \sigma_{k,N}) \quad (5)$$

where $L(I_k|N_k, q_k, \sigma_{k,I})$ is the likelihood function of I_k (all the available relative abundance indices for species k) and it is calculated as $L(I_k|N_k, q_k, \sigma_{k,I}) = \prod_i \prod_t g(I_{i,k,t}|N_{k,t}, q_{i,k}, \sigma_{i,k,I})$. The expression $\pi(N_k|r_k, K_k, \sigma_{k,N})$ is the joint distribution for $(N_k, t = 1981, \dots, 2005)$ and $\pi(N_k|r_k, K_k, \sigma_{k,N}) = \prod_t f(N_{k,t}|N_{k,t-1}, r_k, K_k, \sigma_{k,N})\pi(N_{k,1})$. In Eq. 5, $\pi(q_k, \sigma_{k,I}) = \prod_i \pi(q_{i,k}, \sigma_{i,k,I})$.

$N_{k,1}$ is assumed to follow a uniform distribution between 1% to 100% of K ; The priors for $r_k, K_k, q_{i,k}, \sigma_{k,N}, \sigma_{i,k,I}, N_{k,1}$ are assumed to be independent. Here, scalloped hammerhead shark ($k = 1$) has six indices ($i = 1, \dots, 6$); great hammerhead shark ($k = 2$) has two indices ($i = 1, 4$); and smooth hammerhead shark has only one index ($k = 3$ and $i = 6$).

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

$$p(\theta'|I_{i=1\dots 6, k=1\dots 3}) \propto \prod_k \{L(I_k|N_k, q_k, \sigma_{k,I})\pi(N_k|r_k, K_k, \sigma_{k,N}) \times h(N_{k,1}|\bar{N}_{k,1}, \sigma_{k,N})\pi(r_k|\bar{r}, CV_1)\pi(K_k|K_{\max,k}) \times \pi(K_{\max,k}|\bar{K}_{\max}, CV_2)\pi(q_{i,k}|\bar{q}_i, CV_3) \times \pi(\bar{r})\pi(\bar{K}_{\max})\pi(CV_1)\pi(CV_2)\pi(CV_3)\pi(\bar{q}_i) \times \pi(\sigma_{k,N})\pi(\sigma_{i,k,I})\pi(\bar{N}_{k,1})\}. \quad (6)$$

In the above equations, $\theta' = r_k, K_k, \sigma_{k,N}, \sigma_{i,k,I}, \bar{N}_{k,1}, \bar{r}, \bar{K}_{\max,k}, K_{\max}, q_{i,k}, \bar{q}_i, CV_1, CV_2, CV_3$, and k ranges from one to three species, and i ranges from one to six relative abundance indices. $\bar{N}_{k,1}$ is the median expectation of $N_{k,1}$ and is assumed to follow a uniform distribution between 1% to 100% of K_k . The term $f(N_{k,t}|N_{k,t-1}, r_k, K_k, \sigma_{k,N})$ is the probability density function (pdf) of $N_{k,t}$ given $N_{k,t-1}$ and parameters $r_k, K_k, \sigma_{k,N}$; $g(I_{i,k,t}|N_{k,t}, q_{i,k}, \sigma_{i,k,I})$ is the pdf of $I_{i,k,t}$ given variable $N_{k,t}$ and parameters $q_{i,k}, \sigma_{i,k,I}$; $\pi(r_k|\bar{r}, CV_1)$ is the pdf of r_k given \bar{r} and CV_1 ; $\pi(K_k|K_{\max,k})$ is the pdf of K_k given $K_{\max,k}$; $\pi(K_{\max,k}|\bar{K}_{\max}, CV_2)$ is the pdf of $K_{\max,k}$ given \bar{K}_{\max}, CV_2 ; $\pi(\bar{r})$ and $\pi(\bar{K}_{\max})$ are the pdf’s of \bar{r} and \bar{K}_{\max} ; $\pi(\bar{q}_i)$, $\pi(CV_1)$, $\pi(CV_2)$, $\pi(CV_3)$, $\pi(\sigma_{k,N})$, $\pi(\sigma_{i,k,I})$, and $\pi(\bar{N}_{k,1})$ are the pdf’s of \bar{q}_i and CV_s ($s = 1, 2, 3$), $\sigma_{k,N}$, $\sigma_{i,k,I}$, and $\bar{N}_{k,1}$.

We used WinBUGS, a numerically intensive software package that implements general Bayesian models using

TABLE 2. Goodness-of-fit for the five models expressed as deviance information criterion (DIC).

Scenario	Species	M1	M2	M3	M4	M5
S1	all	117.47	113.99	111.15	122.33	120.69
	scalloped	76.80				
	great	35.86				
	smooth	4.81				
S2	all	117.74	112.09	113.40	121.00	121.09
	scalloped	76.89				
	great	37.02				
	smooth	3.83				
S3	all	117.21	112.26	112.27	121.81	121.61
	scalloped	75.96				
	great	36.92				
	smooth	4.33				
S4	all	115.94	108.73	109.56	120.95	120.80
	scalloped	76.38				
	great	35.30				
	smooth	4.26				
S5	all	121.67	115.07	110.41	120.52	122.65
	scalloped	77.23				
	great	38.81				
	smooth	5.63				
S6	all	118.64	116.74	116.05	122.81	122.16
	scalloped	76.31				
	great	37.81				
	smooth	4.52				
S7	all	117.47	114.87	109.53	120.96	120.94
	scalloped	76.80				
	great	35.86				
	smooth	4.81				

Note: Both total and species-specific DIC values are given for M1.

Markov chain Monte Carlo (MCMC) for model fitting (Gills 1996, Millar and Meyer 2000, Spiegelhalter et al. 2004). The computing code is available in the Supplement.

A critical issue in using MCMC methods is how to determine when random draws have converged to the posterior distribution. Here, three methods were used: monitoring the trace for key parameters, diagnosing the autocorrelation plot for key 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). In this study, three chains were used. 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 then used to avoid parameter autocorrelation and another 20 000 iterations were run to generate the posterior distributions. The posterior distributions of the key parameters were obtained through a kernel smoothing approach available in MATLAB (Bowman and Azzalini 1997, MathWorks 2010).

Sensitivity analysis

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 (M2 and M3) and the r in the nonhierarchical models (M1; Tables 1 and 2). In scenario 1 of the hierarchical models, the

TABLE 3. Posterior estimates of r and K under seven scenarios for each of five Bayesian state-space surplus production models and hammerhead shark species.

Model and species	S1	S2	S3	S4
M1				
Scalloped	$r(0.10, 0.34, 0.68)$ $K(99, 215, 1136)$	$r(0.15, 0.43, 0.88)$ $K(83, 179, 597)$	$r(0.14, 0.46, 0.93)$ $K(81, 159, 578)$	$r(0.10, 0.33, 0.66)$ $K(101, 233, 1177)$
Great	$r(-0.06, 0.17, 0.56)$ $K(187, 487, 3155)$	$r(-0.05, 0.22, 0.79)$ $K(171, 435, 2820)$	$r(-0.04, 0.24, 0.84)$ $K(161, 416, 3137)$	$r(-0.05, 0.18, 0.57)$ $K(187, 486, 2821)$
Smooth	$r(-0.11, 0.15, 0.56)$ $K(28, 89, 677)$	$r(-0.10, 0.20, 0.70)$ $K(26, 82, 352)$	$r(-0.11, 0.18, 0.83)$ $K(23, 90, 663)$	$r(-0.11, 0.15, 0.56)$ $K(30, 89, 457)$
M2				
Scalloped	$r(0.07, 0.24, 0.53)$ $K(111, 246, 1150)$	$r(0.01, 0.24, 0.58)$ $K(110, 251, 1145)$	$r(0.09, 0.25, 0.54)$ $K(110, 238, 1363)$	$r(0.08, 0.24, 0.49)$ $K(109, 202, 977)$
Great	$r(0.05, 0.19, 0.47)$ $K(194, 374, 1533)$	$r(0.01, 0.19, 0.51)$ $K(187, 364, 2318)$	$r(0.05, 0.20, 0.51)$ $K(195, 381, 2113)$	$r(0.06, 0.19, 0.45)$ $K(199, 394, 2341)$
Smooth	$r(0.05, 0.20, 0.47)$ $K(28, 57, 224)$	$r(0.01, 0.20, 0.51)$ $K(27, 58, 301)$	$r(0.06, 0.21, 0.52)$ $K(28, 61, 254)$	$r(0.05, 0.20, 0.44)$ $K(29, 60, 274)$
M3				
Scalloped	$r(0.08, 0.24, 0.51)$ $K(112, 227, 1010)$	$r(0.08, 0.26, 0.53)$ $K(111, 214, 1036)$	$r(0.07, 0.27, 0.57)$ $K(108, 203, 962)$	$r(0.07, 0.24, 0.50)$ $K(119, 245, 1204)$
Great	$r(0.05, 0.19, 0.46)$ $K(199, 409, 1575)$	$r(0.06, 0.21, 0.50)$ $K(195, 356, 1268)$	$r(0.05, 0.21, 0.53)$ $K(183, 382, 1402)$	$r(0.05, 0.18, 0.46)$ $K(200, 428, 1855)$
Smooth	$r(0.06, 0.19, 0.49)$ $K(28, 62, 231)$	$r(0.06, 0.20, 0.48)$ $K(28, 57, 229)$	$r(0.05, 0.21, 0.50)$ $K(28, 62, 246)$	$r(0.05, 0.20, 0.46)$ $K(29, 62, 251)$
M4				
Scalloped	$r(0.05, 0.20, 0.43)$ $K(123, 247, 1418)$	$r(0.05, 0.20, 0.42)$ $K(130, 242, 769)$	$r(0.03, 0.19, 0.44)$ $K(118, 252, 1141)$	$r(0.05, 0.18, 0.39)$ $K(130, 285, 1303)$
Great	$r(0.04, 0.17, 0.41)$ $K(112, 236, 1299)$	$r(0.04, 0.16, 0.44)$ $K(112, 253, 1786)$	$r(0.03, 0.16, 0.42)$ $K(116, 250, 1194)$	$r(0.04, 0.16, 0.38)$ $K(120, 265, 1135)$
Smooth	$r(0.03, 0.15, 0.39)$ $K(34, 74, 339)$	$r(0.03, 0.14, 0.40)$ $K(33, 80, 534)$	$r(0.02, 0.14, 0.37)$ $K(35, 86, 323)$	$r(0.02, 0.14, 0.35)$ $K(35, 90, 423)$
M5				
Scalloped	$r(0.06, 0.20, 0.41)$ $K(123, 250, 1062)$	$r(0.06, 0.20, 0.44)$ $K(128, 263, 886)$	$r(0.06, 0.20, 0.44)$ $K(124, 303, 1400)$	$r(0.05, 0.18, 0.42)$ $K(125, 265, 1320)$
Great	$r(0.04, 0.16, 0.40)$ $K(116, 256, 1472)$	$r(0.05, 0.16, 0.40)$ $K(117, 250, 1174)$	$r(0.05, 0.16, 0.40)$ $K(118, 267, 1470)$	$r(0.04, 0.16, 0.40)$ $K(110, 243, 1379)$
Smooth	$r(0.04, 0.14, 0.33)$ $K(37, 86, 378)$	$r(0.03, 0.15, 0.38)$ $K(37, 88, 507)$	$r(0.03, 0.15, 0.38)$ $K(35, 75, 276)$	$r(0.03, 0.14, 0.36)$ $K(36, 89, 421)$

Notes: Values in parentheses are the 2.5% percentile, median, and 97.5% percentile. K values are in thousands.

hyperprior distribution of \bar{r} was from the meta-analysis of 80 shark species and stocks; in scenario 2, the hyperparameter of variance in the hyperprior distribution was five times that from the meta-analysis ($\bar{r} \sim N(a_1, 5 \times a_2)$); in scenario 3, \bar{r} was assumed to be between -0.2 and 1 . The fourth scenario consisted of increasing the upper bound of \bar{K}_{\max} to 356 770 000, i.e., 10 times the estimated carrying capacity of large coastal sharks. Our fifth scenario was to increase the variance of \bar{r} five times and the upper bound of \bar{K}_{\max} to 356 770 000. Our sixth scenario involved widening CV_s , $\sigma_{k,N}$, and $\sigma_{i,k,N}$, and the seventh scenario was to widen \bar{q}_i in the hierarchical Bayesian models to a uniform distribution $U(0.00001, 10)$, or q_i if q_i is not hierarchically structured to $U(0.00001, 10)$.

Model goodness-of-fit and model selection

The goodness-of-fit of each of the Bayesian hierarchical surplus production models was compared to that of the traditional nonhierarchical surplus production model based on the values of the DIC:

$$DIC = 2\bar{D} - \hat{D} = \bar{D} + p_D$$

$$D(y, \theta) = -2 \log \text{likelihood}(y|\theta)$$

$$p_D = \bar{D} - \hat{D} \quad (7)$$

where D is deviance, a measurement of prediction goodness for our models, p_D is the effective number of parameters in a Bayesian model, \bar{D} is the posterior mean of the deviance, and \hat{D} is the deviance of the posterior mean. Here, y is $I_{i,k}$ and θ includes all the parameters in the corresponding models. The DIC is a hierarchical modeling generalization of the AIC (Akaike information criterion) and BIC (Bayesian information criterion, 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 (Spiegelhalter et al. 2002, 2004). The DIC values for the nonhierarchical models (M1) were computed as the sum of the DIC values from each individual species-specific model.

TABLE 3. Extended.

S5	S6	S7
$r(0.13, 0.42, 0.88)$ $K(86, 165, 580)$ $r(-0.04, 0.23, 0.79)$ $K(167, 396, 2024)$ $r(-0.11, 0.17, 0.69)$ $K(26, 96, 555)$	$r(0.11, 0.37, 0.71)$ $K(92, 176, 668)$ $r(-0.05, 0.18, 0.56)$ $K(190, 480, 2596)$ $r(-0.11, 0.15, 0.55)$ $K(29, 97, 532)$	$r(0.10, 0.34, 0.68)$ $K(99, 215, 1136)$ $r(-0.05, 0.17, 0.56)$ $K(187, 487, 3155)$ $r(-0.11, 0.15, 0.56)$ $K(28, 89, 677)$
$r(0.07, 0.26, 0.60)$ $K(109, 212, 772)$ $r(0.05, 0.20, 0.50)$ $K(191, 365, 1541)$ $r(0.05, 0.21, 0.51)$ $K(28, 58, 276)$	$r(0.08, 0.25, 0.51)$ $K(114, 212, 879)$ $r(0.04, 0.19, 0.44)$ $K(199, 376, 1754)$ $r(0.03, 0.18, 0.44)$ $K(30, 62, 262)$	$r(0.07, 0.24, 0.53)$ $K(111, 246, 1150)$ $r(0.05, 0.19, 0.47)$ $K(194, 374, 1533)$ $r(0.05, 0.20, 0.47)$ $K(28, 57, 224)$
$r(0.09, 0.26, 0.57)$ $K(109, 224, 894)$ $r(0.06, 0.21, 0.1)$ $K(192, 375, 1366)$ $r(0.06, 0.21, 0.51)$ $K(29, 57, 234)$	$r(0.04, 0.22, 0.52)$ $K(123, 260, 1409)$ $r(0.02, 0.18, 0.46)$ $K(195, 372, 1277)$ $r(0.01, 0.19, 0.46)$ $K(29, 61, 256)$	$r(0.08, 0.24, 0.51)$ $K(112, 227, 1010)$ $r(0.05, 0.19, 0.46)$ $K(199, 409, 1575)$ $r(0.06, 0.19, 0.49)$ $K(28, 62, 231)$
$r(0.05, 0.21, 0.47)$ $K(118, 249, 1066)$ $r(0.04, 0.17, 0.46)$ $K(107, 237, 1340)$ $r(0.03, 0.16, 0.39)$ $K(35, 74, 319)$	$r(0.04, 0.20, 0.46)$ $K(118, 259, 1032)$ $r(0.03, 0.17, 0.48)$ $K(105, 237, 2222)$ $r(0.00, 0.13, 0.37)$ $K(36, 86, 378)$	$r(0.05, 0.18, 0.40)$ $K(132, 268, 1117)$ $r(0.04, 0.16, 0.40)$ $K(116, 250, 16923)$ $r(0.03, 0.14, 0.36)$ $K(36, 84, 439)$
$r(0.05, 0.19, 0.40)$ $K(132, 260, 1340)$ $r(0.04, 0.16, 0.38)$ $K(115, 256, 1207)$ $r(0.03, 0.14, 0.36)$ $K(35, 82, 390)$	$r(0.05, 0.18, 0.39)$ $K(122, 255, 1189)$ $r(0.04, 0.15, 0.43)$ $K(114, 245, 1160)$ $r(0.03, 0.14, 0.36)$ $K(36, 87, 397)$	$r(0.05, 0.18, 0.40)$ $K(128, 265, 1213)$ $r(0.04, 0.15, 0.40)$ $K(115, 254, 1453)$ $r(0.03, 0.14, 0.35)$ $K(38, 78, 350)$

Model robustness is also often considered when comparing hierarchical and nonhierarchical models (Roberts and Rosenthal 2001) because model selection based on fit can only be inconclusive, especially when differences in DIC values are less than 5 (Spiegelhalter et al. 2002, Jiao et al. 2008, 2009b). We considered both model robustness and fit in our study because of the limited number of groups in the hierarchical model (3).

Under the assumption of a Schaefer population growth model, $N_{\text{msy}} = rK/4$ is the abundance at maximum sustainable yield (msy) and $F_{\text{msy}} = r/2$ is the rate of fishing mortality at msy. The estimated rate of fishing mortality F relative to F_{msy} , F/F_{msy} , and population size relative to N_{msy} , N/N_{msy} , were also compared among different models. The probability of F being larger than F_{msy} , i.e., $P(F > F_{\text{msy}})$ was used to define the risk of overfishing. It indicates the exploitation status of the population. The probability of N being smaller than N_{msy} , i.e., $P(N < N_{\text{msy}})$ was used to define the risk of a population being overfished. It is a measure of the depletion level of the population and its present status in terms of abundance.

RESULTS

Hierarchical models with a two-level prior of r (M2) and two-level priors of r and K (M3) yielded smaller DIC values (108–116) than nonhierarchical models (M1; 115–122; Table 2). However, hierarchical models with r and q (M4) or r , K , and q hierarchically structured (M5) resulted in larger DIC values (120–123) than for M1, M2, and M3 (Table 2), thus consistently yielding the worst fit of the five models tested. The DIC values and parameter estimates can be influenced by the choice of priors as reflected by their variation among sensitivity scenarios (Tables 2 and 3). Although there were differences among DICs the differences were limited between M2 and M3.

The hierarchical models were very robust to the hyperparameters. Parameters r and K varied very little when the variance of the hyperparameter of r was multiplied by factors of 5 (scenario 2) with respect to that used in scenario 1. The nonhierarchical models were less robust than the hierarchical models (Fig. 3). Similar results were found when the distribution of \bar{r} was less informative, with a wide uniform distribution (scenario 3) and when both the variance of the hyperparameter of r and the upper bound of \bar{K}_{max} were increased by a factor of 5 and 10, respectively (scenario 5). Results seemed less sensitive to changes in the upper bound of \bar{K}_{max} (scenarios 2, 4 and 5). Results from scenario 4 were close to those of scenario 1 even though the upper bound of the prior \bar{K}_{max} increased by a factor of 10 (Table 3 and Fig. 3).

When model M1 was used, a less informative distribution of r resulted in higher posterior values of r and lower posterior values of K (scenarios 2, 3, and 5; Table 3; Fig. 3). Less informative prior distributions of K (scenarios 4 and 5), or q_i (scenario 7), did not substantially influence results. However, all of the hierarchical models were very robust to the less informative distributions of both r and K (Table 3; Fig. 3).

Models M2 and M3 resulted in similar results in both parameters and population size estimation; while models M4 and M5 resulted in similar results but the results were somewhat different compared to these from M2 and M3 (Figs. 3 and 4). Models M2 and M3 resulted in higher posterior r values for these three species than when using M4 or M5 (Table 3; Fig. 3A). The posterior of K for great hammerhead was noticeably lower for M4 and M5 than for M1 to M3 (Table 3; Fig. 3B). The posterior population size estimates for great hammerhead shark were lower when M4 and M5 were used than when M2 and M3 were used (Fig. 4).

When K_k was not hierarchically structured (M2), the resulting DIC values were close to those for the hierarchical structured K_k (M3), and model results were very similar. Increasing the upper bound of K_k , i.e., $K_{\text{max},k}$ from c_2 to 10 times the value of c_2 did not change appreciably the estimates of r or K . This indicated that the estimated carrying capacity of large coastal sharks (NMFS 2006) is a large enough quantity to be the upper bound of K_k .

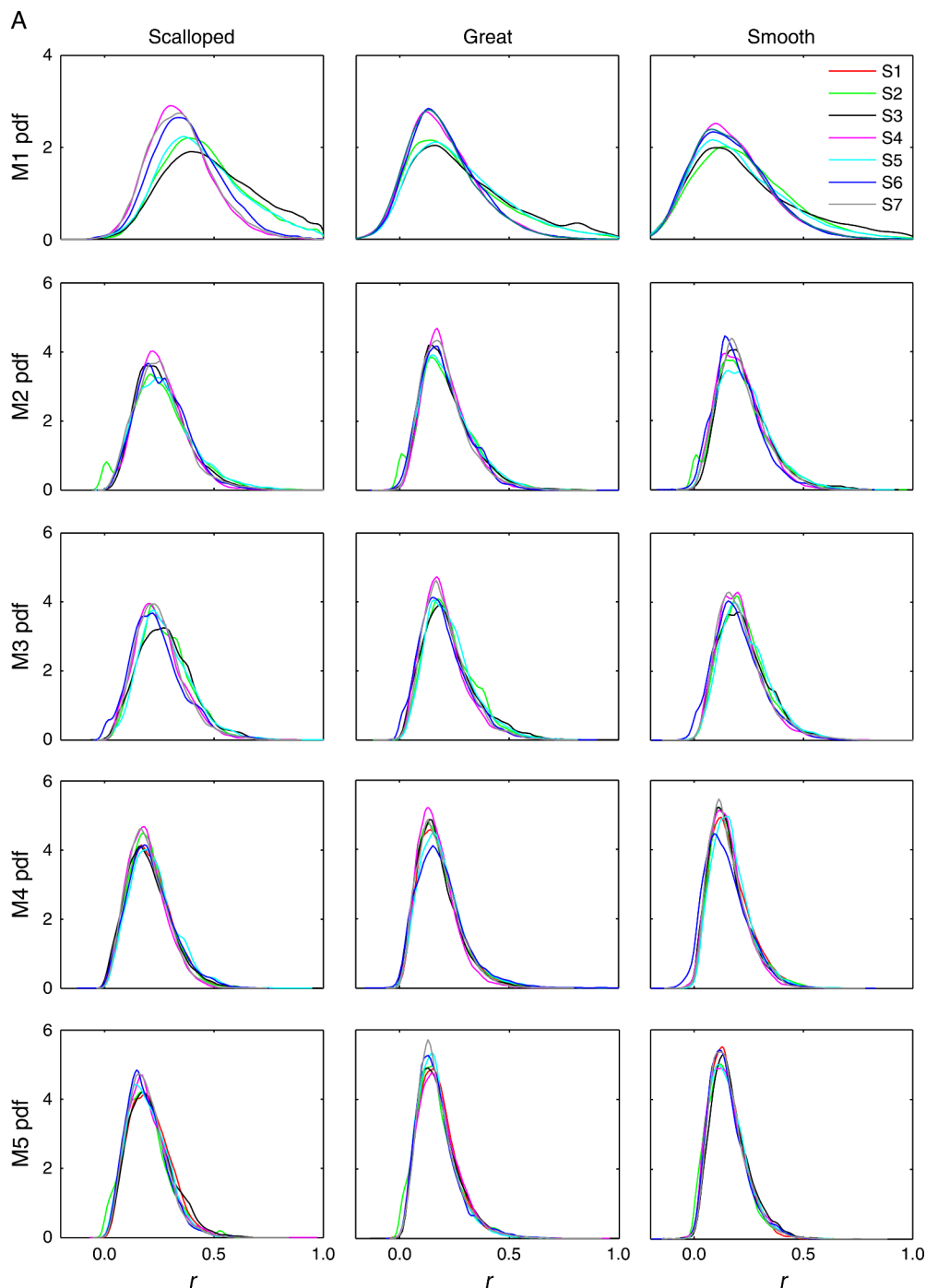


FIG. 3. Probability density functions (pdfs) of (A) growth rate (r) and (B) carrying capacity (K) from the five models under seven scenarios (S1–S7) for the three hammerhead shark species.

The three methods we used failed to show evidence against convergence of the MCMC algorithm. The Gelman and Rubin statistic for all parameters, including all variance terms, ranged from 0.95 to 1.01, indicating convergence of the Markov chains. The autocorrelation function plot indicated a thinning interval of 5, which was large enough to address potential autocorrelation in

the MCMC runs (figures are not shown). We also visually observed the trace plots of the major parameters, which showed good mixing of the three chains, also indicative of convergence of the MCMC chains.

The Bayesian hierarchical state-space surplus production models, M2 to M4, fitted the data reasonably well (Fig. 5). The population of scalloped hammerhead likely

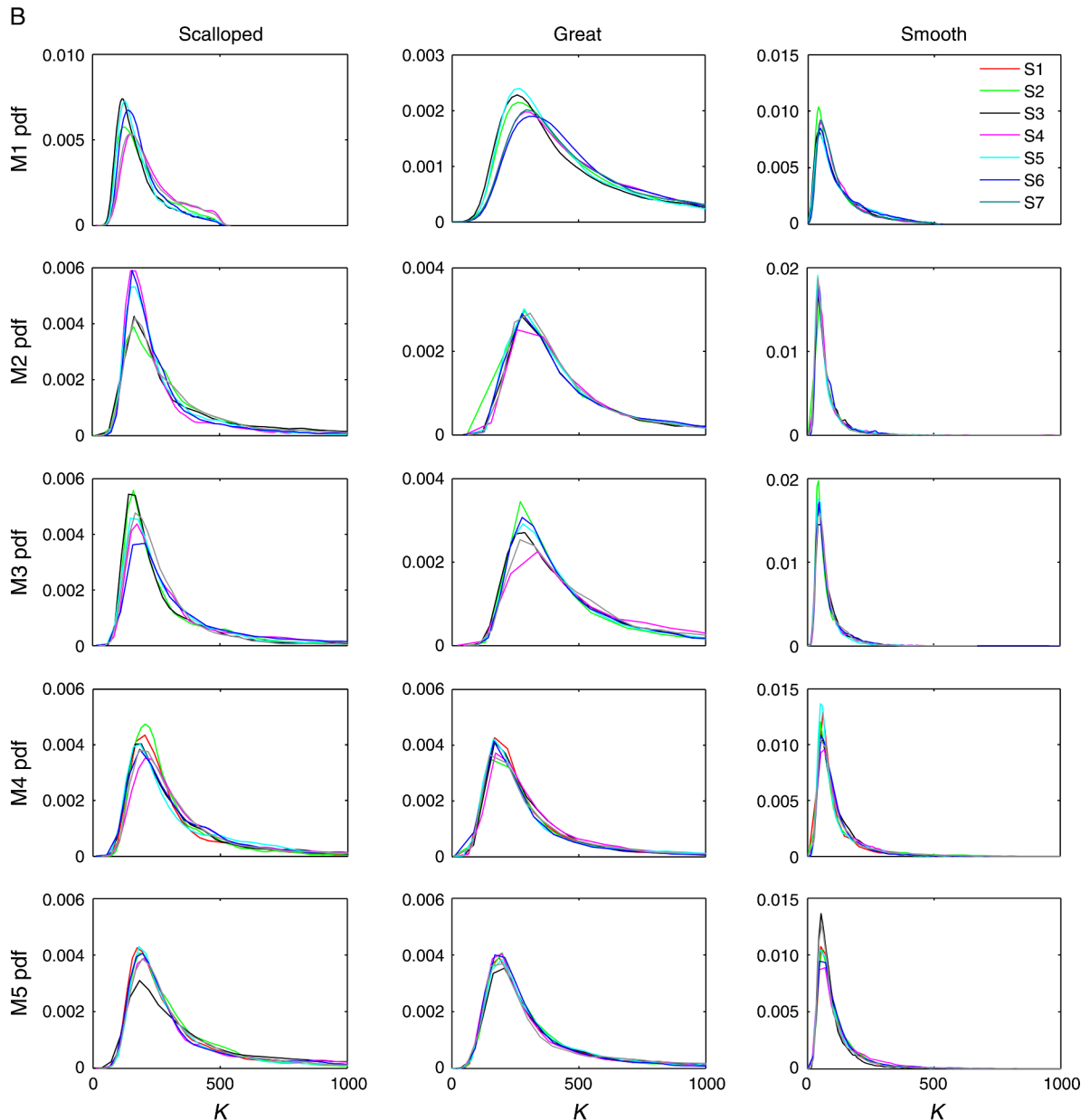


FIG. 3. Continued.

became overfished from the early 1980s and overfishing occurred periodically from 1983 to 2005; the risk of overfishing was still high in recent years (Fig. 6). The population of great hammerhead likely became overfished in the mid-1980s and overfishing occurred periodically from 1983 to 1997; the risk of overfishing was very low after 2001 (Fig. 6). The population of smooth hammerhead likely become overfished since mid-1980s but the degree of overfishing was not as high that for scalloped hammerhead sharks until the mid-1990s and overfishing occurred continuously in 1994–1998, but the risk of overfishing was generally very low after 2001 (Fig. 6).

DISCUSSION

The goodness of fit (DIC values) of the hierarchical models M2 to M3 were the lowest and the differences between them were very limited. The DICs of M4 and M5 were higher than that of the nonhierarchical model (M1) for all three species considered, likely because of the limited number of species (three) hierarchically structured in our study. The limited differences in DIC values between M2 and M3, and between M4 and M5, prescribed the need for using multiple criteria to compare model performance instead of using information-based criteria only. Use of less informative priors

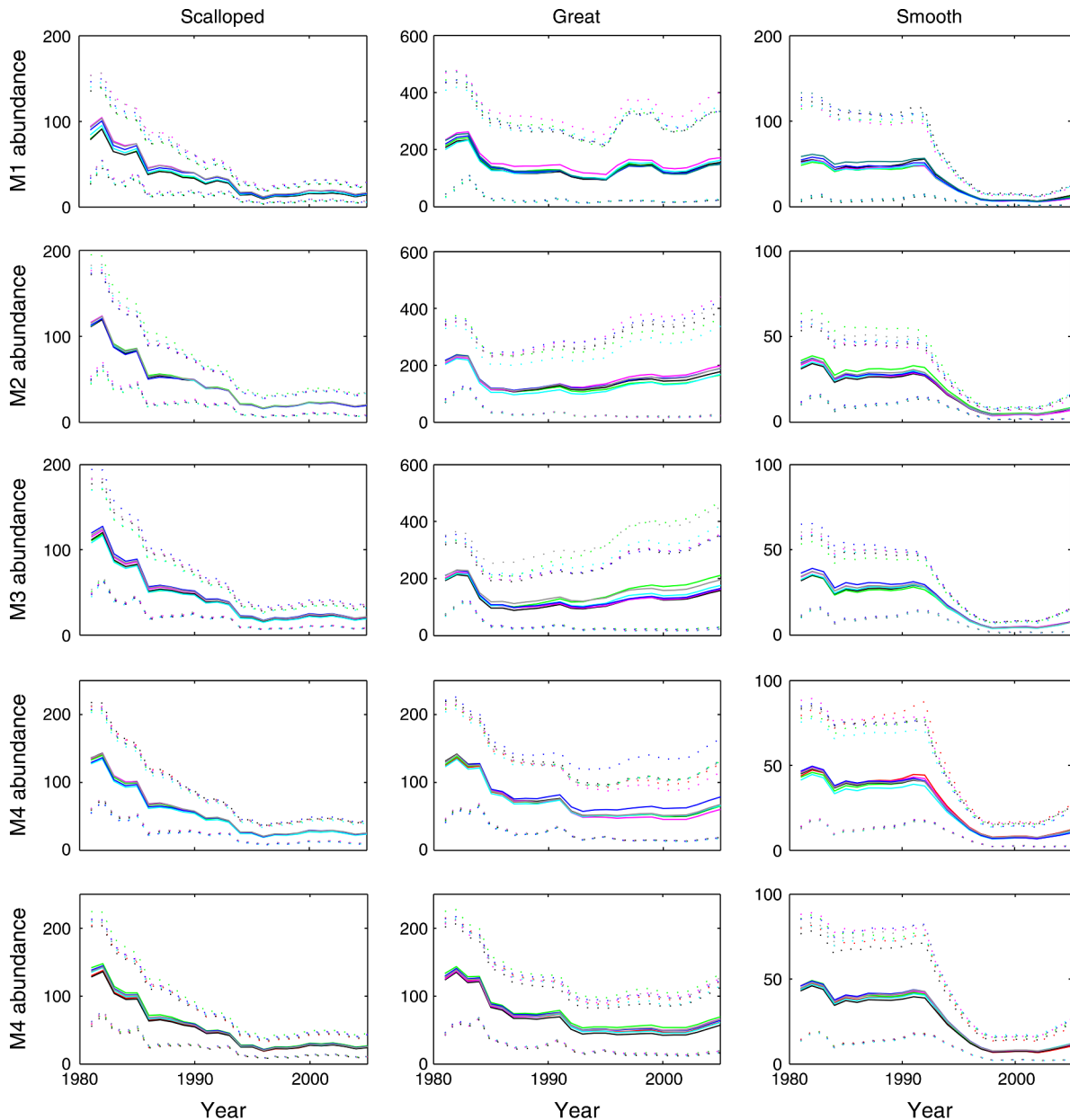


FIG. 4. Population abundance trajectories (in thousands of fish) for scalloped, great, and smooth hammerhead sharks. Solid lines denote the posterior mean of population abundance; dotted lines denote 95% credible intervals of population abundance. Different scenarios are denoted by different colors, which have the same meaning as in Fig. 3.

for the means of r , K , or q and associated variances consistently yielded robust results with the hierarchical models. The robustness of the results indicated that even when using uninformative priors with a limited number of species, the hierarchical models were still useful and are a convenient approach for data-poor species to borrow strength from more data-rich species. A recent study on protein interactions based on a likelihood approach and three species also indicated the advantages of using multiple organisms and hierarchical models (Liu et al. 2005).

The sensitivity analyses conducted showed that hierarchical Bayesian models (with a multilevel prior of r , r and q , r and K , or r , K , and q) provided a more robust fit to the hammerhead data than nonhierarchical models. This suggests that a hierarchical Bayesian model or the use of multilevel priors is mathematically viable and valuable in modeling these three hammerhead shark populations and potentially other fish complexes for which species-specific data are available. However, this study also revealed that informative priors influence the results of both model parameters

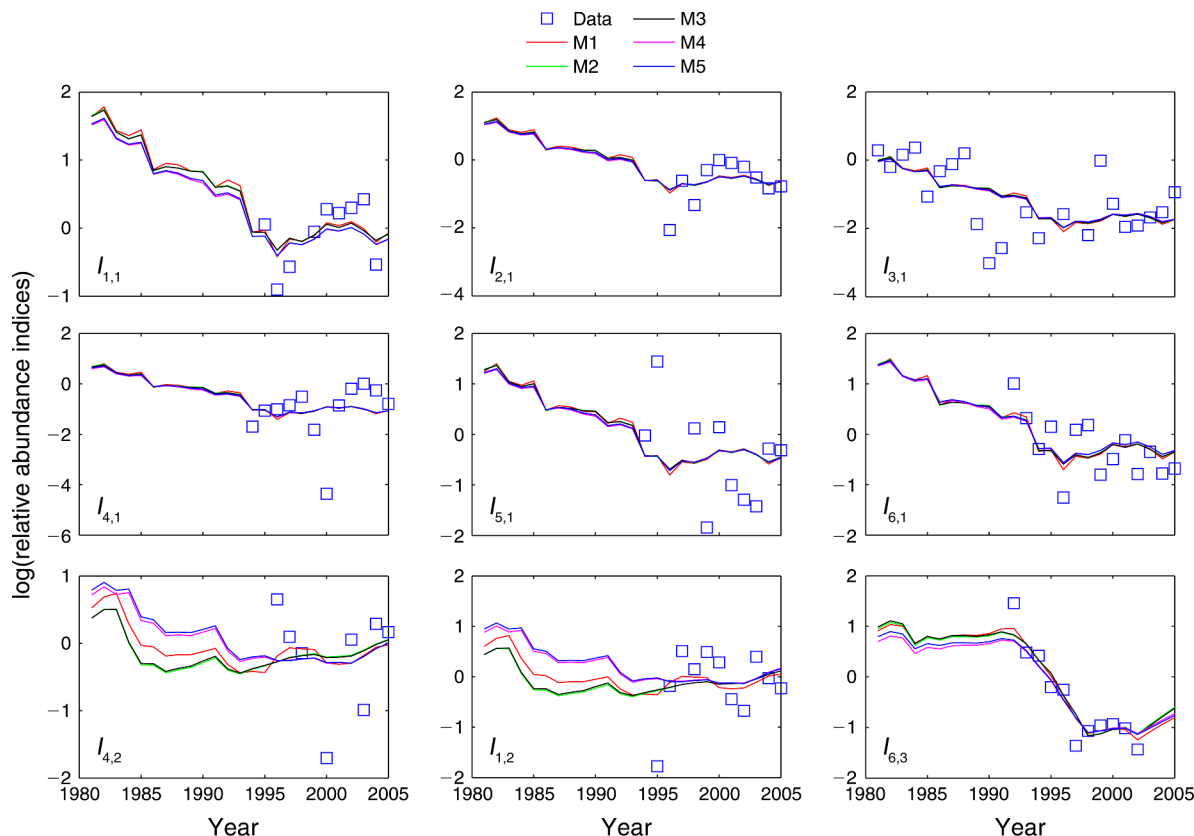


FIG. 5. Model fits to the logarithm of relative abundance indices from the five models under scenario 1. See *Methods: Bayesian state-space surplus production model for each species* for description of indices $I_{i,k}$.

and model fit (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 in the fish complex. In all, both the model goodness-of-fit and the fact that the Bayesian hierarchical model with a multilevel prior of r (M2) resulted in robust results for all three species in the complex suggest that this model is a better choice.

Although the results from M4 and M5 with r and q or r , K , and q hierarchically structured were also robust to prior specification, the DIC values were higher than those of the nonhierarchical models (M1). This suggests that M4 and M5 were not as good a choice as M2, possibly because of lack of informative priors on q_i . However, although DIC values of M4 and M5 were larger, the pdf profiles were narrower and modeling results for great and smooth hammerheads tended to be more biologically reasonable, with M4 and M5 estimating smaller population growth rates than M2 and M3. 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 (E. Cortés, *unpublished data*). Future studies that allow specification of informative priors are thus recommended. In addition to gaining a better under-

standing of the biology of these three species and specifying more informative priors on catchability (q), Bayesian model averaging could be used as an alternative method that would allow model M4 and M5 to still be considered given that it was robust and the DIC values were not much larger than that of the nonhierarchical model (M1) (Spiegelhalter et al. 2002, Jiao et al. 2008, 2009b).

Multilevel priors are robust priors given the stability of the model results (Roberts and Rosenthal 2001). Our study showed consistent results across seven scenarios with multilevel priors. Compared with the commonly used priors, multilevel priors therefore may be better choices as robust priors. The number of levels of priors will depend on the parameters of interest and biological reality. For example, here we were interested in the population growth rate r rather than hyperparameter \bar{r} ; hence we had two levels of hyperparameters, which resulted in a stable distribution of r . We were also aware that the mean of r_k can be different among species. Thus, a multilevel prior of r reflects the biology of the fish species and allows the data-poor species to borrow strength from data-rich species. The resulting distributions of r_k for both data-rich and data-poor species were more stable and showed uncertainty reduction when hierarchical mod-

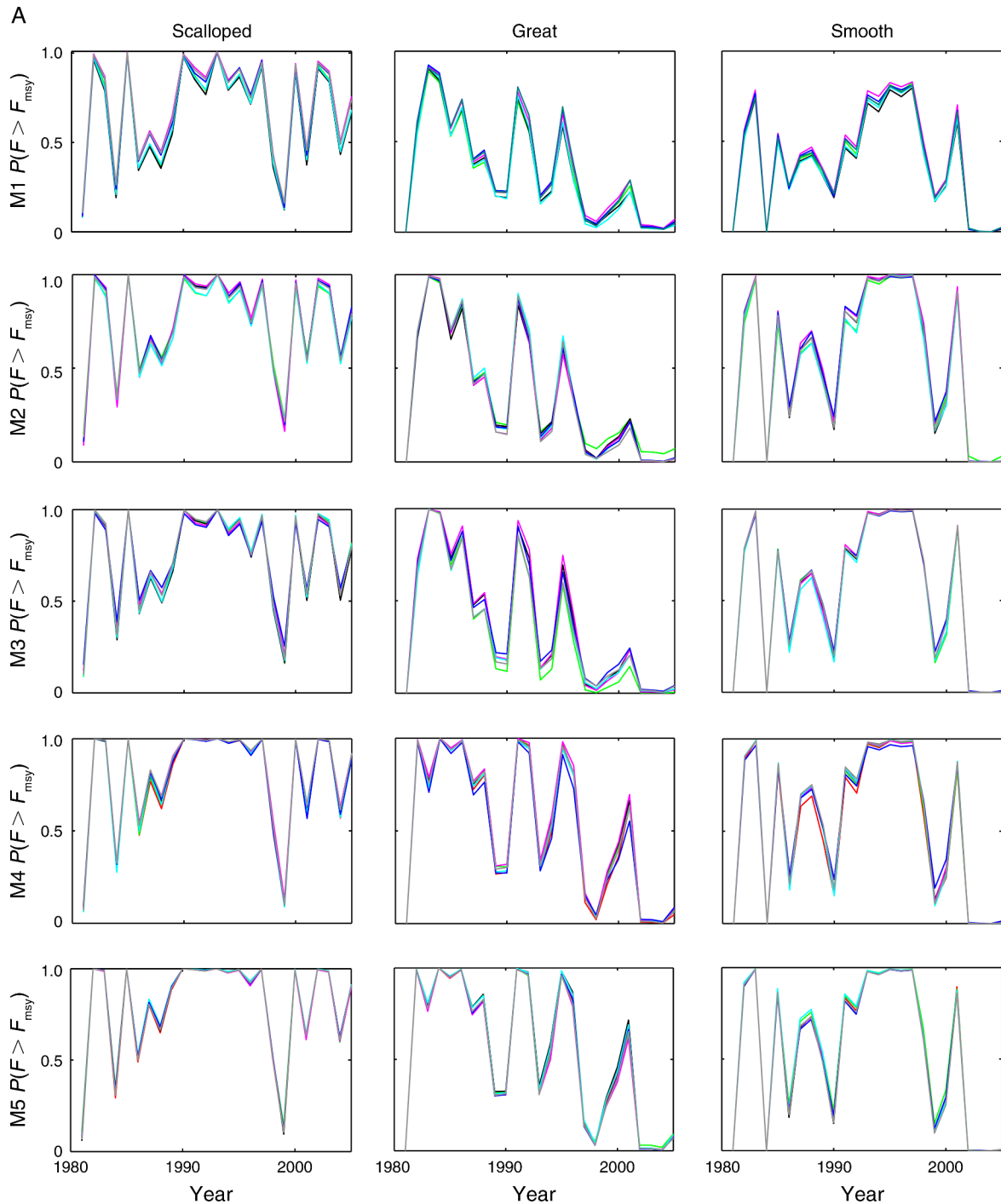


FIG. 6. (A) Probability of fishing mortality, F , being larger than F_{msy} and (B) probability of population size, N , being smaller than N_{msy} for the three hammerhead shark species under seven scenarios, where the subscript msy denotes the value at maximum sustainable yield. Different scenarios are denoted by different colors, which are the same as in Fig. 3.

els were used. This indicated that the hierarchical models benefit not just the data-poor species but also the data-rich species.

It is a common perception that MCMC output should be thinned to reduce autocorrelation (Gelman et al. 2004, Spiegelhalter et al. 2004). However, to estimate

posterior quantities, it has been proven that thinning is suboptimal (MacEachern and Berliner 1994). We reran the models and scenarios with a thinning interval of 2 and 0, respectively, but the results were the same as with a thinning interval of 5. Although most Bayesian analyses still use thinning in MCMC to eliminate

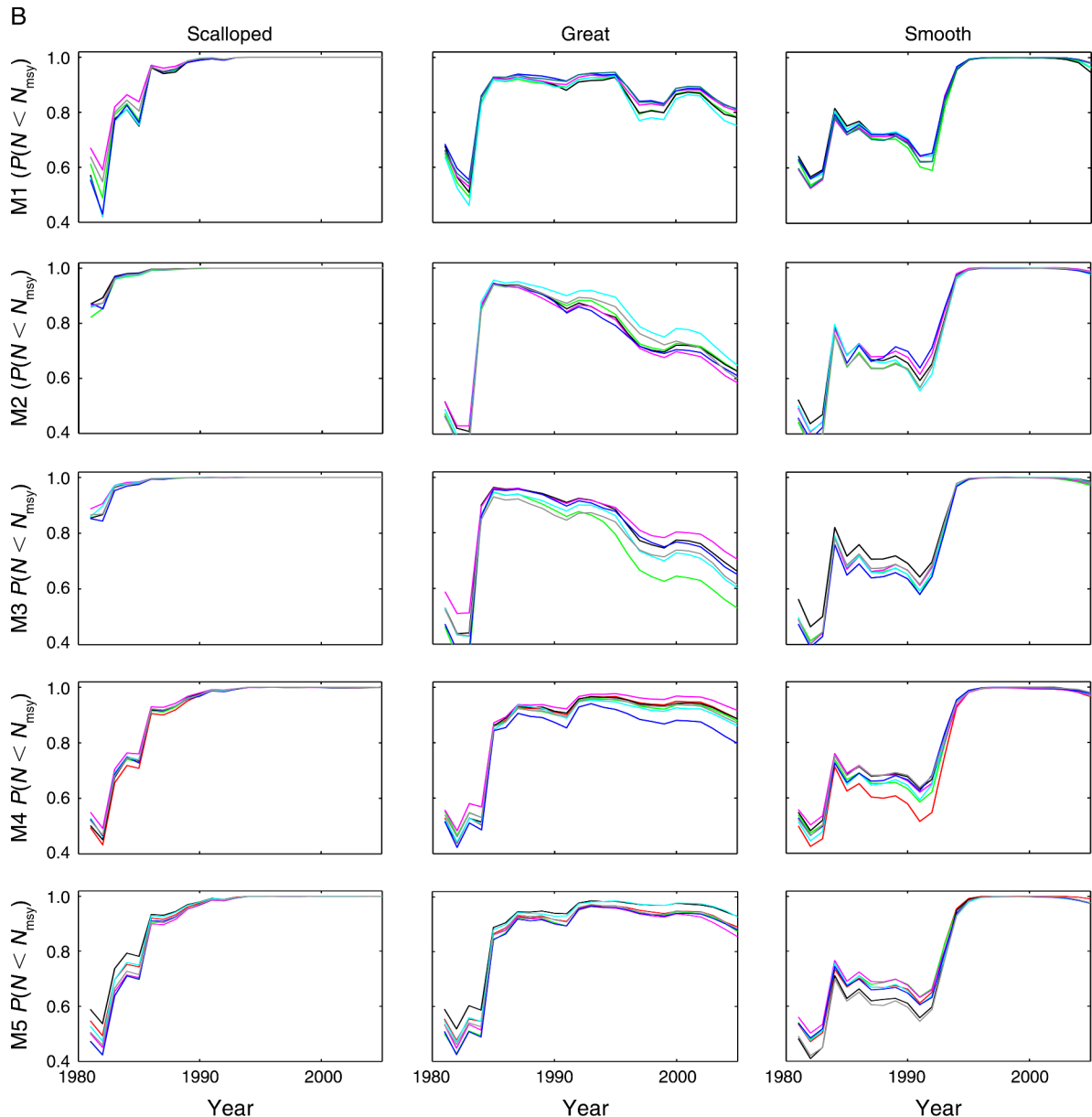


FIG. 6. Continued.

autocorrelation of the Markov chains, whether thinning should be used or not was beyond the scope of our study.

The DIC is widely used to compare hierarchical models (Spiegelhalter et al. 2002, 2004, Jiao et al. 2009b). However, other criteria, such as the posterior likelihood ratio and posterior predictive p values have also been proposed for model checking and/or comparison (Meng 1994, Aitken et al. 2005). These other criteria have been found to provide conclusions that are consistent with those derived by frequentist theory. Application of these alternative Bayesian criteria in

applied ecological modeling should be further investigated.

The hierarchical 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 in some cases (Beamish et al. 1999, Clark 2003). There is evidence that even intraspecific population growth rates, r_k , can vary over time as a consequence of climate variation, for example (Beamish et al. 1999, Peterman et al. 2003, Jiao et al. 2008). Although variation of the intraspecific population growth rate was not the main reason for using hierarchical models in our case, the



PLATE 1. Chris Hayes holds a great hammerhead shark as it is tagged in the National Marine Fisheries Service, Pascagoula Lab shark bottom longline research cruise. Photo credit: Dana Bethea.

stability and more reasonable biological results for the scalloped hammerhead shark population may be a reflection of using hierarchical models.

Traditionally used likelihood or frequentist methods often require prior knowledge on the process and/or observation errors or the ratio of process to observation error. However, in this study we used the Bayesian approach, which does not necessarily need prior knowledge on the variances (Millar and Meyer 2000, Calder et al. 2003, Carroll et al. 2006). The Bayesian approach has been found to be very efficient in identifying the variances in state-space models. Simulations would further help identify the ability of this approach to accurately estimate process error and observation error. A recent simulation study (He 2010) found that state-space models with both process and observation error considered provided the best estimates (in terms of accuracy and precision) of the key parameters of the models and the population sizes.

We emphasize that the purpose of our study was to present a new approach for assessing data-poor and poor-data stocks. The results of the hammerhead shark stock assessment that we present as an example should thus be viewed as illustrative rather than as conclusive evidence of their present status. To that end, a more systematic study investigating a variety of data and analytical issues should be conducted.

Hierarchical Bayesian models allow poor-data species to borrow strength from species with good-quality data and have been applied to small-area, small-sample size estimation problems (Berger 1985, He and Sun 1998, 2000, Su et al. 2001, Gelman et al. 2004). Many hierarchical modeling analyses based on empirical data showed the advantages of using multilevel analysis because it allows years and/or locations with poor data to borrow strength from years and/or locations with better data (He and Sun 2000, Su et al. 2001, Gelman et al. 2004). It is thus important for researchers in the field of fisheries to become more acquainted with the application of Bayesian hierarchical models for data-poor and poor-data species.

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SUPPLEMENT

WinBUGS codes for the models used in the paper (*Ecological Archives* A021-120-S1).