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Population dynamics modelling with spatial heterogeneity for yellow croaker (*Larimichthys polyactis*) along the coast of China

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Abstract

As one of the top four commercially important species in China, yellow croaker (*Larimichthys polyactis*) with two geographic subpopulations, has undergone profound changes during the last several decades. It is widely comprehended that understanding its population dynamics is critically important for sustainable management of this valuable fishery in China. The only two existing population dynamics models assessed the population of yellow croaker using short time-series data, without considering geographical variations. In this study, Bayesian models with and without hierarchical subpopulation structure were developed to explore the spatial heterogeneity of the population dynamics of yellow croaker from 1968 to 2015. Alternative hypotheses were constructed to test potential temporal patterns in yellow croaker's population dynamics. Substantial variations in population dynamics characteristics among space and time were found through this study. The population growth rate was revealed to increase since the late 1980s, and the catchability increased more than twice from 1981 to 2015. The East China Sea's subpopulation witnesses faster growth, but suffers from higher fishing pressure than that in the Bohai Sea and Yellow Sea. The global population and two subpopulations all have high risks of overfishing and being overfished according to the MSY-based reference points in recent years. More conservative management strategies with subpopulation considerations are imperative for the fishery management of yellow croaker in China. The methodology developed in this study could also be applied to the stock assessment and fishery management of other species, especially for those species with large spatial heterogeneity data.

Key words: yellow croaker, population dynamics, Bayesian hierarchical model, geographic variation

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1 Introduction

Stock assessment could provide decision-makers with suggestions on the consequences of alternative management strategies (Jensen, 2005; Punt and Hilborn, 1997). These suggestions include predictions of the reactions between stocks and fishers to diverse levels of fishing pressure, and estimating the fishing effort level to obtain the maximum sustainable yield (MSY). One of the most associated models with MSY is the surplus production model, developed by Schaefer in 1954 (Schaefer, 1954).

Surplus production models (SPM), also known as biomass dynamics models or surplus yield models, rely on an assumption that a stock could produce an excess or surplus biomass (or abundance) that can be harvested. The SPM is assumed to combine the change of the stock's biomass (except the fishing mortality), including the individual growth in weight, the recruitment of new individuals and the natural mortality (Quinn and Deriso, 1999). SPMs can provide inferences of the relationships between fishing effort to population biomass and catch, and estimate the biological reference points, such as MSY, fishing mortality and effort to achieve MSY (Jensen, 2005). The most important merit of this kind of model is their minimum requirement of data, i.e., they can be modelled with just the time series data of catch and abundance index. These models can be applied in fisheries without substantial size-structure, biological, selectivity or other survey data. These models are suitable in cases where other assessment methods with huge amount of data requirement are not feasible.

Yellow croaker (*Larimichthys polyactis*) is one of the top four most important fish species in China. Its annual catch ranges between 343 000–400 000 t in recent years and brings about 540 million of dollars to Chinese fisheries economy (Bureau of Fisheries and Fishery Administration of Ministry of Agriculture, 1969–2016). However, only time series data of fishery catch and effort are available for this species with a coarse spatial and temporal resolution (i.e., yearly data of each province) in the past 48

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years (Bureau of Fisheries and Fishery Administration of Ministry of Agriculture, 1969–2016). As a result, surplus production models are likely to be the most appropriate stock assessment approach of yellow croaker populations along the coast of China.

Yellow croakers are widely distributed in the Northwest Pacific Ocean, including the coastal waters of China, Korea and Japan. In China, its natural habitat extends from the Bohai Sea, Yellow Sea to the East China Sea, across 22°–41°N. The existence of geographic subpopulations for yellow croaker in China has been confirmed by previous studies based on the differences in life history, body morphometries, migration trajectories, etc. (Lin et al., 1965; Liu, 1990; Xu and Chen, 2010; Zhang et al., 2014). The hypothesis of two subpopulations, the Bohai Sea and Yellow Sea subpopulation, and the East China Sea subpopulation, is widely accepted (Xu and Chen, 2010; Zhang et al., 2014). Their migration indicates little interactions between these two subpopulations, characterized with differences in spawning, feeding and wintering grounds (Xu and Chen, 2010). Therefore, it is essential to consider the spatial heterogeneity in the studies for yellow croaker.

No long term coastal wide population dynamics assessment has been explored so far for this important species. Two existing stock assessments for the East China Sea subpopulation of yellow croaker used surplus production models to evaluate fishery status and population status (Li et al., 2011, Liu et al., 2013). However, both of them used short-term time series data (1991–2003 and 1999–2008, respectively) and only considered observation error in their model construction. Potential variations on its population dynamics caused by long term environmental changes and fishing pressure have been reflected in its life history changes and fishing behavior, such as early maturity and increased catchability, but they have never been considered in the population dynamics and stock assessment (Jin, 1996; Jiao et al., 2006, 2008; Shan et al., 2011; Yan et al., 2014). A comprehensive study on the population dynamics of yellow croaker is critically needed to analyze the long-term subpopulation dynamics under multiple pressures.

This study tends to investigate geographical variations in the population dynamics of two subpopulations of yellow croaker, i.e., the Bohai Sea and Yellow Sea subpopulation (BYSS) and the East China Sea subpopulation (ECSS), using fishery data back to late the 1960s. Bayesian hierarchical state-space surplus-production models have been implemented to describe the population dynamics in most previous researches (Jiao et al., 2009a, 2011; Li and Jiao, 2015). The hierarchically structured models with spatial heterogeneity could be used to address the variability of population parameters among subpopulations that have been reflected in life history variation and fishery characteristics changes (Li and Jiao, 2015). These models could test hypotheses on its population dynamics characteristics and potential catchability variations (Jiao et al., 2006, 2008). Based on these results, conservative management strategies with spatial considerations would be discussed and suggested for the management of yellow croaker fishery in China.

2 Materials and methods

2.1 *Data sources*

Time series catch and effort data of yellow croaker were extracted from *China Fishery Statistical Yearbooks* from 1968 to 2015 (Bureau of Fisheries and Fishery Administration of Ministry of Agriculture, 1969–2016). Catch record given in 10^5 t, and the power of fishing vessels in 10^7 kW were used as proxies for fishing effort (Fig. 1). Data included both national and province-specific data for catch and effort. The yellow croaker fishery in Shandong Province and its northern provinces targeted BYSS, while that in Jiangsu Province and its southern provinces targeted ECSS.

Generally, China's catches for yellow croaker kept at low levels (0.21×10^5–0.55×10^5 t) from 1968 to 1989, then appeared to increase reaching the highest value (4.07×10^5 t) in 2010, and slightly decreased in the subsequent five years (Fig. 1). Temporal trends in respective catches for the two subpopulations (BYSS and ECSS) were much similar, which were kept at low level during the first 23 years and increased after 1990. The fishing effort increased in these 48 years for both the whole population and the two subpopulations, except in 1991 when the effort decreased abruptly (Fig. 1). The geographical difference in the population parameters and overall dynamics among the two subpopulations of yellow croaker were evaluated in this study (Fig. 2).

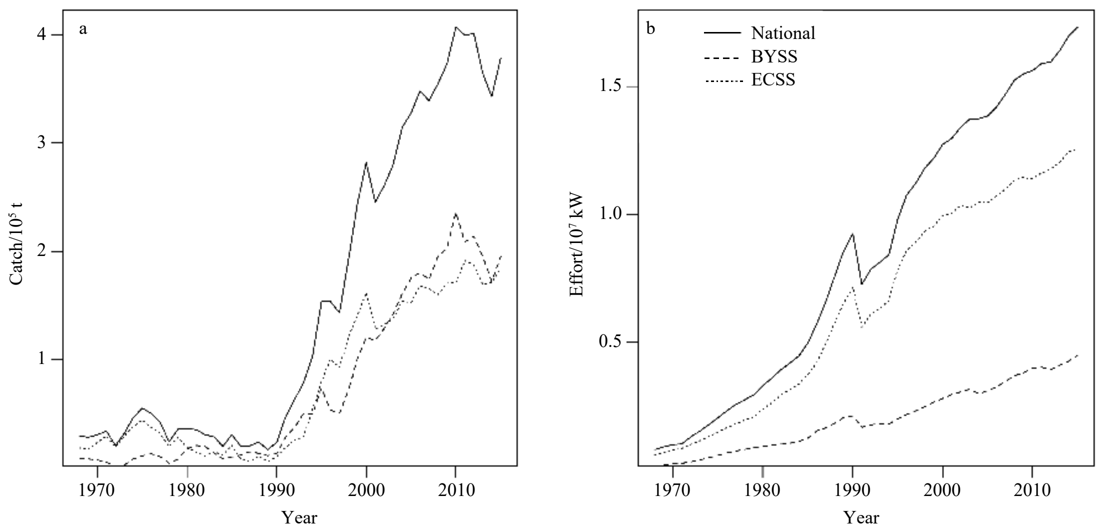

Fig. 1. The catch and effort of the whole population and two subpopulations of yellow croaker in China seas from 1968 to 2015. BYSS is the Bohai Sea and Yellow Sea subpopulation, and ECSS the East China Sea subpopulation.

2.2 *Population dynamics model*

The basic model structure was the state-space surplus production model:

$$B_{t+1} = (B_t + f(B_t) - C_t) \times e^{\sigma_{1,t}}, \tag{1}$$

$$\frac{C_t}{E_t} = CPUE_t = q \times B_t \times e^{\sigma_{2,t}}, \tag{2}$$

where B_t is the stock biomass in year t; C_t is the total catch; E_t is the effort in year t; $CPUE_t$ is the catch per unit effort in year t (10^{-2} t/kW); and q is the catchability coefficient. The observation-process-error estimator used in this study, considered both the observation error in the function of CPUE and the process error in the function of stock biomass (Prager, 1994; de Valpine and Hastings, 2002).

The likelihood function for B is

$$L\left(B|\theta_1\right) = \prod_{1968}^{2014} \frac{1}{B_t\sigma_1\sqrt{2\pi}} \times \exp\left\{\frac{\left[\ln B_{t+1} - \ln(B_t + f(B_t) - C_t)\right]^2}{2\sigma_1^2}\right\}. \tag{3}$$

The likelihood function for $CPUE$ is

$$L\left(CPUE|\theta_2\right) = \prod_{1968}^{2015} \frac{1}{CPUE_t\sigma_2\sqrt{2\pi}} \times \exp\left\{\frac{\left[\ln CPUE_t - \ln\left(qB_t\right)\right]^2}{2\sigma_2^2}\right\}. \tag{4}$$

In the above two likelihood functions, θ_1 and θ_2 represent all the parameters in Eqs (1) and (2), respectively.

Schaefer model was used for the production function $f(B_t)$, which is the most widely used and accepted surplus production model (Schaefer, 1954):

$$f(B_t) = rB_t\left(1 - \frac{B_t}{K}\right), \tag{5}$$

in which, r is the growth rate parameter (derived from the intrinsic rate of natural increase), and K represents the carrying capacity.

In the basic global model, yellow croaker was assumed to be one population along the coast of China without subpopulation-specific considerations.

$$K \sim \ln N\left(\ln\bar{K}, v_K\right) T\left(K_1, K_2\right); \bar{K} \sim U\left(4, 10\right); v_K \sim U\left(0, 1\right), \tag{6}$$

$$r \sim \ln N\left(\ln\bar{r}, v_r\right); \bar{r} \sim U\left(0.6, 0.8\right); v_r \sim U\left(0, 1\right), \tag{7}$$

$$q \sim U\left(q_{\_L}, q_{\_U}\right). \tag{8}$$

The carrying capacity K and growth rate r were assumed to follow lognormal distribution (ln$N$), with hyperparameters mean and variance. The values of K were limited to be higher than the maximum catch ($K_1=4\times10^5$ t) and lower than five times of the maximum catch ($K_2=5\times4\times10^5$ t), given the reality that it is a heavily fished species. The hyperparameter $\bar{K}$ was set to follow uniform distribution between 4×10^5 t and 10×10^5 t, since K for yellow croaker subpopulation in the East China Sea was estimated to be about 3.9×10^5 t (Li et al., 2011). The hyperparameter $\bar{r}$ was set to follow uniform distribution between 0.6 and 0.8, which should be at least larger than the natural mortality (0.49 from Lin et al. (2006)) to keep the population survive. As the biomass was between the maximum of catch and the carrying capacity, and K was between max(catch) and 5×max(catch), the catchability q (CPUE/biomass) should be between the lower level $q_{\_L}$=CPUE/(5×max(catch) and the upper level $q_{\_U}$=CPUE/min(catch). The expectation of biomass in 1966 was assumed to follow uniform distribution between 70% and 100% of K, i.e., $\bar{B}_{1966} \sim U\left(0.7K, K\right)$, based on the Bayesian model setting and the condition of this population (Fisheries Bureau and Yellow Sea Fisheries Headquarters in the Ministry of Agriculture, 1990; McAllister and Kirkwood, 1998). The variance of biomass $v_b=\sigma_1^2$ and the variance of CPUE $v_i=\sigma_2^2$ were all assumed to follow uniform distribution between 0 and 0.5, while other variances were set to follow uniform distribution between 0 and 1.

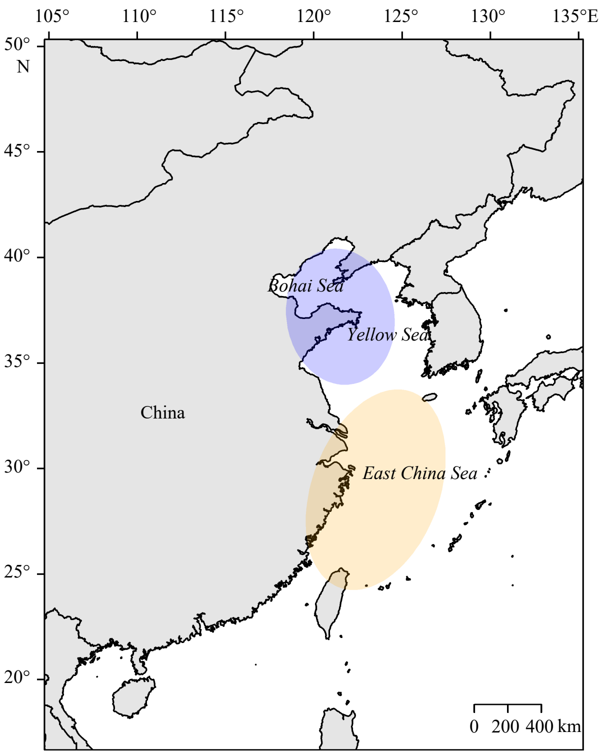

Fig. 2. The main distributions of two yellow croaker subpopulations. The Bohai Sea and Yellow Sea subpopulation distributes in the coastal area covered by the blue ellipse and the East China Sea subpopulation distributes in the coastal area covered by the yellow ellipse.

When the subpopulation-specific data were used to assess population dynamics, instead of modelling each subpopulation separately, a Bayesian hierarchical model was developed to assess the two subpopulations simultaneously (Parent and Rivot, 2012). In the hierarchical models, all three parameters (K, r and q) were assumed to be hierarchically structured, following lognormal distributions (Table 1).

$$K_i \sim \ln N\left(\ln\bar{K}, v_K\right) T\left(K_{1i}, K_{2i}\right), \tag{9}$$

$$r_i \sim \ln N\left(\ln\bar{r}, v_r\right), \tag{10}$$

$$q_i \sim \ln N\left(\ln\bar{q}, v_q\right) T\left(q_{\_Li}, q_{\_Ui}\right), \tag{11}$$

in which i is the subscript for subpopulations, with i=1 for BYSS and i=2 for ECSS.

The population size, structure and growth rate of yellow croaker, have undergone great changes due to the environmental variations and increased fishing pressure (Yan et al., 2014). Thus, the growth rate parameter r was set to be time-varying with random walk in some alternative models (Table 1), which meant r_t following lognormal distribution with mean r_{t-1} and variance v_r:

$$r_{t=1} \sim \ln N\left(\ln\bar{r}, v_r\right); r_t \sim \ln N\left(\ln r_{t-1}, v_r\right), \text{when } t \geqslant 2. \tag{12}$$

Due to the fast-economic development in China since 1980 and the improvement of the fishing technique, the catchability q was assumed to increase after 1980, with the Δq following uniform distribution between 1 and 1.05:

$$q_t = q_{t-1} \times \Delta q_{t-1}; \Delta q_{t-1} \sim U(1, 1.05) \text{ between 1981 and 2015, i.e., } t = 14 \text{ to } 48. \tag{13}$$

Therefore, in both the global models and subpopulation models, there were alternative models in which r or/and q were set to be time-varying. These four alternative models had parameters with constant r and q, time-varying q, time-varying r, as well as time-varying q and r (Table 1).

2.3 *Bayesian methods*

Just Another Gibbs Sampler (JAGS) is an effective program to fit Bayesian models using Markov Chain Monte Carlo (MCMC) (Plummer, 2003). In this study, coda, rjags and runjags packages were used to fit models with JAGS in R version 3.4.3 (Plummer et al., 2006; Denwood, 2016; Plummer, 2016). Except 50 000 burn-in iterations, 100 000 iterations and 3 chains were used to estimate the posterior distributions of parameters with a thinning interval of 100. Different initial values were generated for each chain during the model fitting, and Gelman-Rubin convergence statistic was calculated to diagnose model convergence (Gelman and Rubin, 1992).

In the global model, $p(\theta|CPUE)$, the posterior density for all parameters (θ) given the observations CPUE, can be written as

$$p(\theta|CPUE) \propto L(CPUE|B, q, \sigma_2)\pi(B|r, K, \sigma_1)\pi\left(q, \sigma_2\right)\pi\left(r, K, \sigma_1\right). \tag{14}$$

In the subpopulation hierarchical models, the posterior probability can be expressed as

$$\begin{aligned} p\left(\theta'|CPUE_{i=1,2}\right) \propto \prod_i \{ & L\left(CPUE_i|B_i, q_i, \sigma_{2,i}\right)\pi\left(B_i|r_i, K_i, \sigma_{1,i}\right) \times \\ & \pi\left(K_i|\bar{K}, v_K\right)\pi\left(r_i|\bar{r}, v_r\right)\pi\left(q_i|\bar{q}, v_q\right) \times \\ & \pi\left(\bar{K}\right)\pi\left(\bar{r}\right)\pi\left(\bar{q}\right)\pi\left(v_K\right)\pi\left(v_r\right)\pi\left(v_q\right)\}. \end{aligned} \tag{15}$$

In the above equations, $L(CPUE|B, q, \sigma_2)$ is the likelihood function of CPUE. The expression $\pi(B|r, K, \sigma_1)$ is the joint distribution for biomass from year 1968 to 2015. $\pi(v_K)$ is the probability density function of parameter v_K. i ranges from the first to the second subpopulation.

The performance of Bayesian models was measured based on the Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002), which has been widely used and demonstrated by many previous studies (Jiao et al., 2009b, 2011; Chang et al., 2015; Wang et al., 2016). The DIC can be calculated by

$$\text{DIC} = 2\bar{D} - \hat{D}, \tag{16}$$

$$\bar{D}\left(\theta\right) = E_{\theta|y}\left(-2\ln L(y|\theta)\right), \tag{17}$$

$$\hat{D}\left(\theta\right) = -2\ln L(y|\bar{\theta}), \tag{18}$$

where D is deviance used to measure the prediction of goodness, $\bar{D}$ is the posterior mean of the deviance and $\hat{D}$ is the deviance of the posterior mean. As a hierarchically modelling generalization of the Akaike Information Criterion and Bayesian Information Criterion, lower DIC values indicate better model fitting.

After comparing the four global Bayesian models (M1–M4) and four Bayesian hierarchical models (M5–M8), five scenarios were used to test the sensitivity of the model outcomes respect-

Table 1. Model scenarios, sensitivity analysis, and resulted goodness of fit shown as the Deviance Information Criterions (DICs)

	Model	Description	Prior for $v_{\rm i}$	Prior for $v_{\rm b}$	Scenario	DIC
Global	M1	q and r constant	U(0, 0.5)	U(0, 0.5)		207
Global	M2	r constant, q time-varying	U(0, 0.5)	U(0, 0.5)		184
Global	M3	q constant, r time-varying	U(0, 0.5)	U(0, 0.5)		148
Global	M4	r and q time-varying	U(0, 0.5)	U(0, 0.4)	S1	48
			U(0, 0.5)	U(0, 0.5)	S2	66
			U(0, 0.5)	U(0, 0.7)	S3	66
			U(0, 0.4)	U(0, 0.5)	S4	54
			U(0, 0.7)	U(0, 0.5)	S5	60
Subpopulation	M5	q and r constant	U(0, 0.5)	U(0, 0.5)		528
Subpopulation	M6	r constant, q time-varying	U(0, 0.5)	U(0, 0.5)		132
Subpopulation	M7	q constant, r time-varying	U(0, 0.5)	U(0, 0.5)		136
Subpopulation	M8	r and q time-varying	U(0, 0.5)	U(0, 0.4)	S1	40
			U(0, 0.5)	U(0, 0.5)	S2	47
			U(0, 0.5)	U(0, 0.7)	S3	39
			U(0, 0.4)	U(0, 0.5)	S4	46
			U(0, 0.7)	U(0, 0.5)	S5	61

ively, to the specified priors for the best model scenarios (Table 1). In Scenarios S1–S3, the variance (υ_i) of the CPUE (observation-error) was assumed to follow uniform distribution U(0, 0.5), while the prior distribution of the variance (υ_b) of biomass (process-error) were U(0, 0.4), U(0, 0.5) and U(0, 0.7), respectively. In Scenarios S4 and S5, the prior distribution of variance of CPUE were U(0, 0.4) and U(0, 0.7) respectively, while U(0, 0.5) was for the variance of biomass.

2.4 *Biological reference points*

The fishery biological reference points, including MSY (maximum sustainable yield), $E_{\rm MSY}$, $F_{\rm MSY}$ and $B_{\rm MSY}$ (the fishing effort, fishing mortality and the biomass to achieve MSY, respectively) were computed as follows (Haddon, 2011):

$$\mathrm{MSY} = \frac{rK}{4}; F_{\rm MSY} = \frac{r}{2}; B_{\rm MSY} = \frac{K}{2}; E_{\rm MSY} = \frac{r}{2 \times q}. \tag{19}$$

The risk of overfishing and overfished were defined by the MSY-based reference points, which are the probability of F being greater than $F_{\rm MSY}$, i.e., $P(F>F_{\rm MSY})$, and the probability of the biomass being smaller than $B_{\rm MSY}$, i.e., $P(B<B_{\rm MSY})$, respectively. The probability of E being greater than $E_{\rm MSY}$, $P(E>E_{\rm MSY})$, was also estimated, since the fishing effort was the main control target of the fishery management in China (Cao et al., 2017). The probabilities were estimated as the percentage of iterations where $F>F_{\rm MSY}$, $E>E_{\rm MSY}$ or $B<B_{\rm MSY}$ in the total number of iterations in the Bayesian approach. The depletion was also calculated by the biomass of the most recent year (2015) relative to the carrying capacity K (Caddy, 1998).

3 Results

Among the four global models, Model M4 with time-varying r and q outperformed, which yielded much smaller DIC values than other models (Table 1). The subpopulation Model M8 with time-varying r and q, performed much better than other subpopulation models. Both the global Model M4 and the hierarchical Model M8 were relatively robust to the priors of the observation and process errors. The results were not sensitive to the changes in the upper bound of the noninformative priors of the CPUE and biomass variance under different sensitivity scenarios (Figs 3 and 4).

In Model M4, the posterior population growth rate r values were time-varying, with low level from 1965 to 1985 (median estimates lower than 0.50), and increased sharply to about 2.42–2.66 from 1985 to 2010 in different scenarios, with a little decline in recent five years (Fig. 5). The posterior r values for each subpopulation from Model M8 showed similar trend (Fig. 6), however the r values of ECSS after 1985 was higher than that of BYSS with overlapped 95% credible intervals (95% CI).

The catchability q for the global population and the two subpopulations, kept at low level before 1980, but increased by more than two times from 1981 to 2015. The q of the subpopulation ECSS was much lower than that of BYSS, with non-overlapped 95% CI (Fig. 6). The median of the posterior carrying capacity K for the whole population along the coast of China was 6.74×10^5–7.48×10^5 t in different scenarios. The posterior K for the two subpopulations were much similar, with the median values being 3.78–4.05 and 3.97×10^5–4.05×10^5 t in different scenarios for ECSS and BYSS, respectively.

The Bayesian state-space surplus production models, both M4 and M8, fitted the CPUE data well (Figs 7 and 8). When yellow croaker was assumed as a whole population along the coast of China in Model M4, its posterior estimated biomass decreased from 1966 to 1990, recovered in 1990 and slightly declined during the last decade. Similarly, the biomass for the two subpopulations in Model M8, varied with the same trend. Before 1980, the estimated biomass of the subpopulation BYSS was lower than that of ECSS, while it recovered to better conditions with higher biomass estimates than that of ECSS.

The whole population of yellow croaker likely became overfished ever since the late 1970s and overfishing occurred since from the mid-1970s, with depletion rate varying from 0.26–0.28 in 2015 in different scenarios (Fig. 9 and Table 2). The $P(F>F_{\rm MSY})$ and $P(E>E_{\rm MSY})$ of the whole population showed similar patterns. The subpopulation BYSS became overfished since early 1970s and overfishing occurred ever since the mid-1980s, and the depletion rate observed from 0.36–0.37 (Fig. 10 and Table 2). The subpopulation ECSS became overfished since 1980 and overfishing occurred periodically during the 1980s and absolutely since 1990, and recorded depletion rate in 2015 was 0.19–0.20 (Fig. 10 and Table 2). Estimates of $P(F>F_{\rm MSY})$, $P(E>E_{\rm MSY})$ and $P(B<B_{\rm MSY})$ for the ECSS subpopulation were much higher than those of BYSS in the last 15 years (Fig. 10).

According to the results obtained via Bayesian models, the biological reference points including MSY, $E_{\rm MSY}$, $F_{\rm MSY}$ and $B_{\rm MSY}$ were estimated for both the whole population and the two subpopulations of yellow croaker (Table 2). The MSY for the whole population was 4.19×10^5–4.47×10^5 t according to the global Model M4, while the MSY for the subpopulations BYSS and ECSS were 1.97×10^5–2.00×0^5 and 2.37×10^5–4.43×10^5 t based on the subpopulation Model M8, respectively. The $E_{\rm MSY}$ for the subpopulation ECSS was $0.65\times10^7 0.67\times10^7$ kW in 2015, while the observed fishing effort in 2015 was 1.26×10^7 kW. For the subpopulation BYSS, the observed effort in 2015 was 0.45×10^7 kW, which was much higher than the $E_{\rm MSY}$ 0.28×10^7–0.29×10^7 kW in the same year.

4 Discussion

In this study, the whole yellow croaker population in China seas during the past 48 years was covered with and without considering subpopulation dynamics, which could greatly improve our understanding of the status and dynamics of this species. Bayesian hierarchical models were applied in this study to conduct stock assessment for yellow croaker, considering the spatial and temporal variations of population growth rate and catchability, and provided the biological reference points for the fishery management of yellow croaker. Based on the results of this study, more conservative management strategies with spatial considerations and specific reference points for MSY, biomass and effort, were suggested for the management of yellow croaker fishery in China.

The best Bayesian hierarchical model revealed that the growth rate r and the catchability q of the yellow croaker's population increased over a long time series and showed a large geographical difference. The hierarchical Bayesian models with multilevel priors and time-varying r and q consistently proved to fit the data much better. So, it was suggested to be a mathematically viable and valuable approach in modelling the spatial complex fishery data (Jiao et al., 2008, 2009a). The use of multilevel priors in Bayesian models was found to be a better choice than the commonly used priors because multilevel priors could lead to the stability of model results (Roberts and Rosenthal, 2001; Jiao et al., 2011). The methodology developed and demonstrated in this study also applies to the stock assessment and fishery management of many other species, especially for those species with

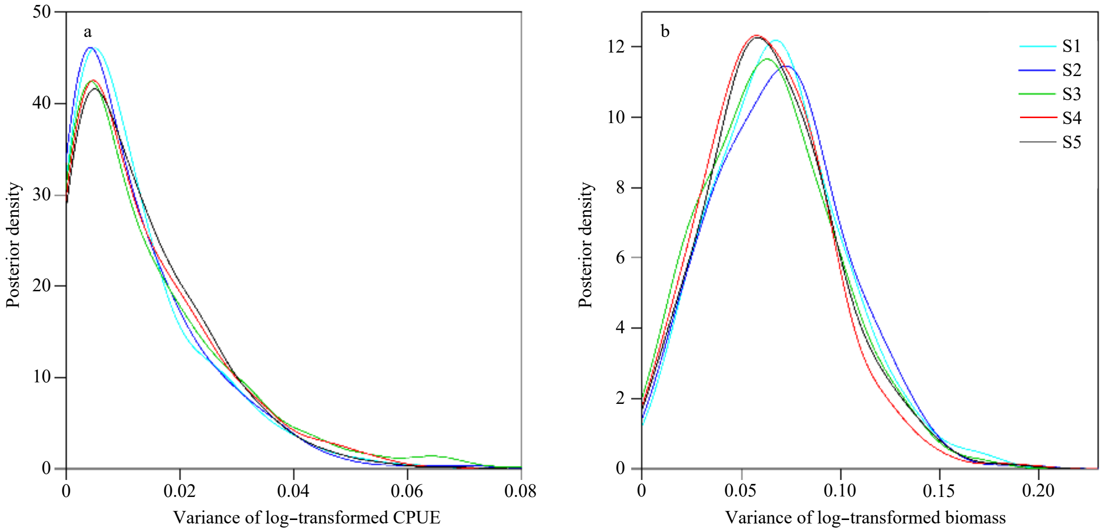

Fig. 3. The posterior distributions for the variance of log-transformed CPUE and the variance of log-transformed biomass under different prior distributions (Scenarios S1–S5) for the model M4. Different scenarios are shown in different colors.

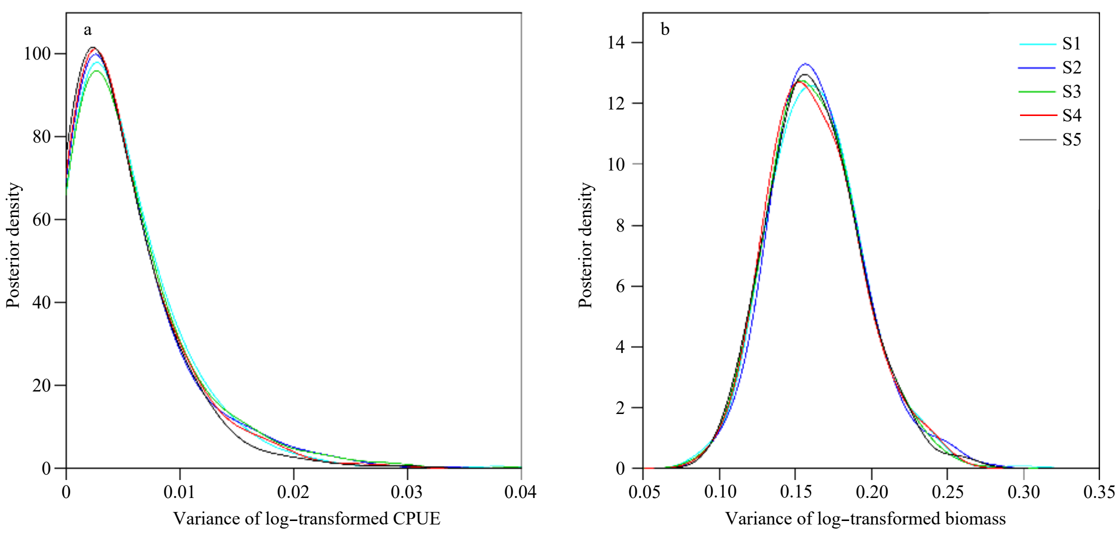

Fig. 4. The posterior distribution for the variance of log-transformed CPUE and the variance of log-transformed biomass under different prior distributions (Scenarios S1–S5) for the subpopulation Model M8. Different scenarios are shown in different colors.

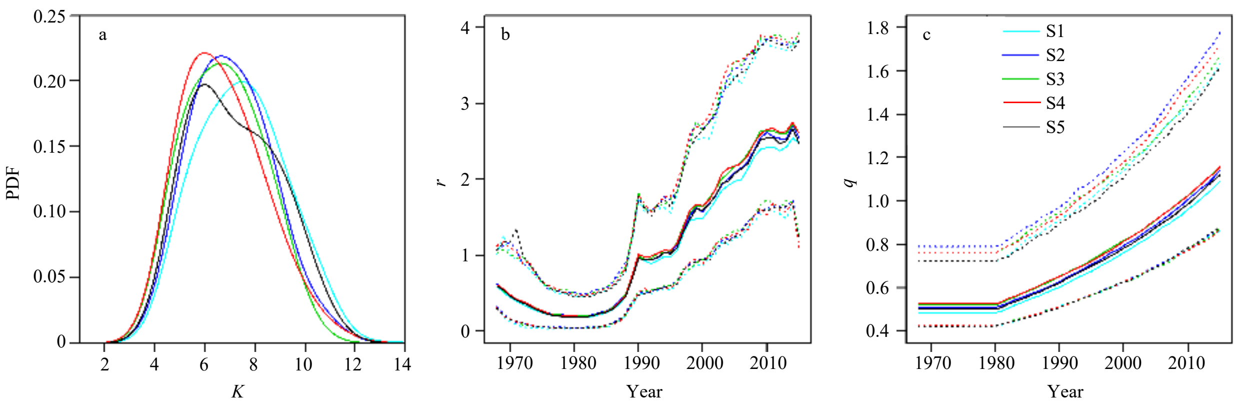

Fig. 5. The posterior estimates of coefficients (K, r and q) from the global Model M4 for yellow croaker. PDF indicates the probability density functions, solid lines the posterior medians, and dotted lines the 95% credible intervals. Different scenarios (S1–S5) are shown in different colors.

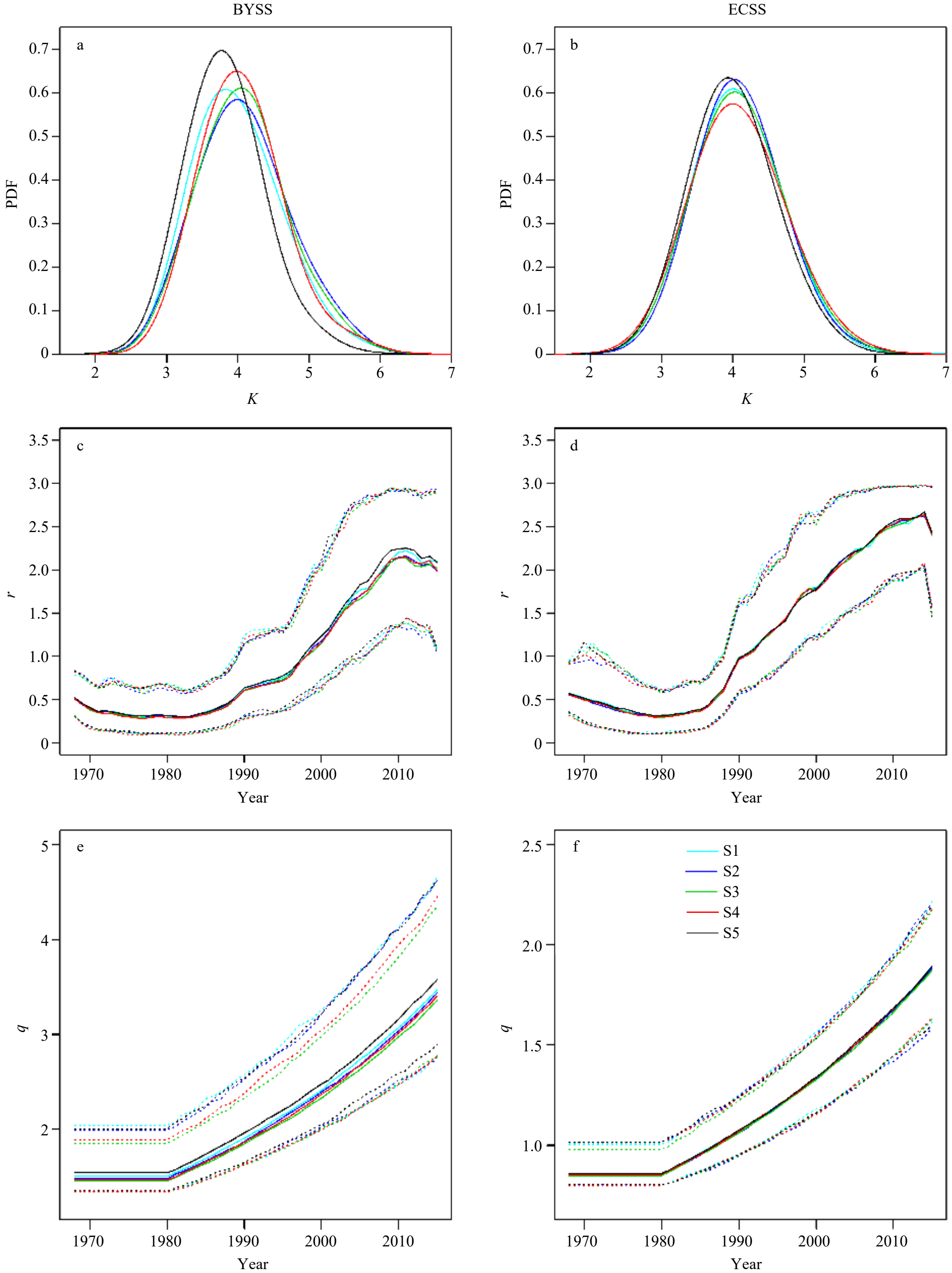

Fig. 6. The posterior estimates of coefficients (K, r and q) from the subpopulation Model M8 for two yellow croaker subpopulations. BYSS is the Bohai Sea and Yellow Sea subpopulation, and ECSS the East China Sea subpopulation. Solid lines represent the posterior medians and dotted lines the 95% credible intervals. Different scenarios (S1–S5) are shown in different colors.

large spatial heterogeneity and limited fishery data, as is the case with most fishery in China.

The population growth rate was not assumed to be constant, which allowed the investigation of its variation over time to likely be related to regime shifts and changes in productivity regimes (Beamish et al., 1999; Jiao, 2009; Clark, 2003). Both data fitting and the improved fishing techniques confirmed the increasing pattern of the catchability q. Thus, the growth rate r and catchability q of yellow croaker might exhibit some variations caused by the intensive fishing activities and catch technique improvements, and should not be assumed consistent in the model.

The population of yellow croaker in China has depleted under high fishing pressure. Under this circumstance, the growth rate of this species might increase to survive and recover its pop-

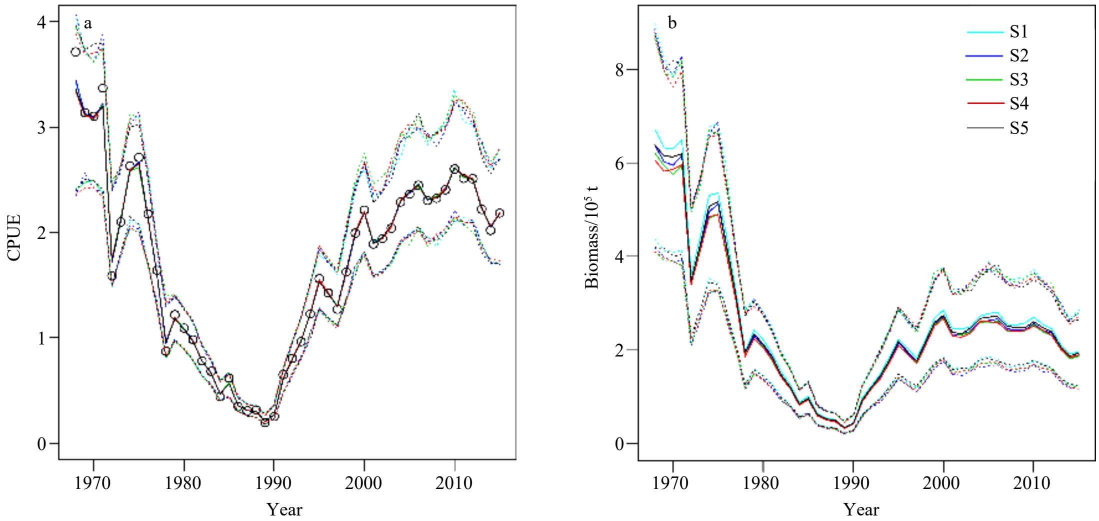

Fig. 7. The estimates of CPUE and biomass for yellow croaker from the global Model M4. Dots represent observation data, solid lines the posterior medians, and dotted lines the 95% credible intervals. Different scenarios (S1–S5) are shown in different colors.

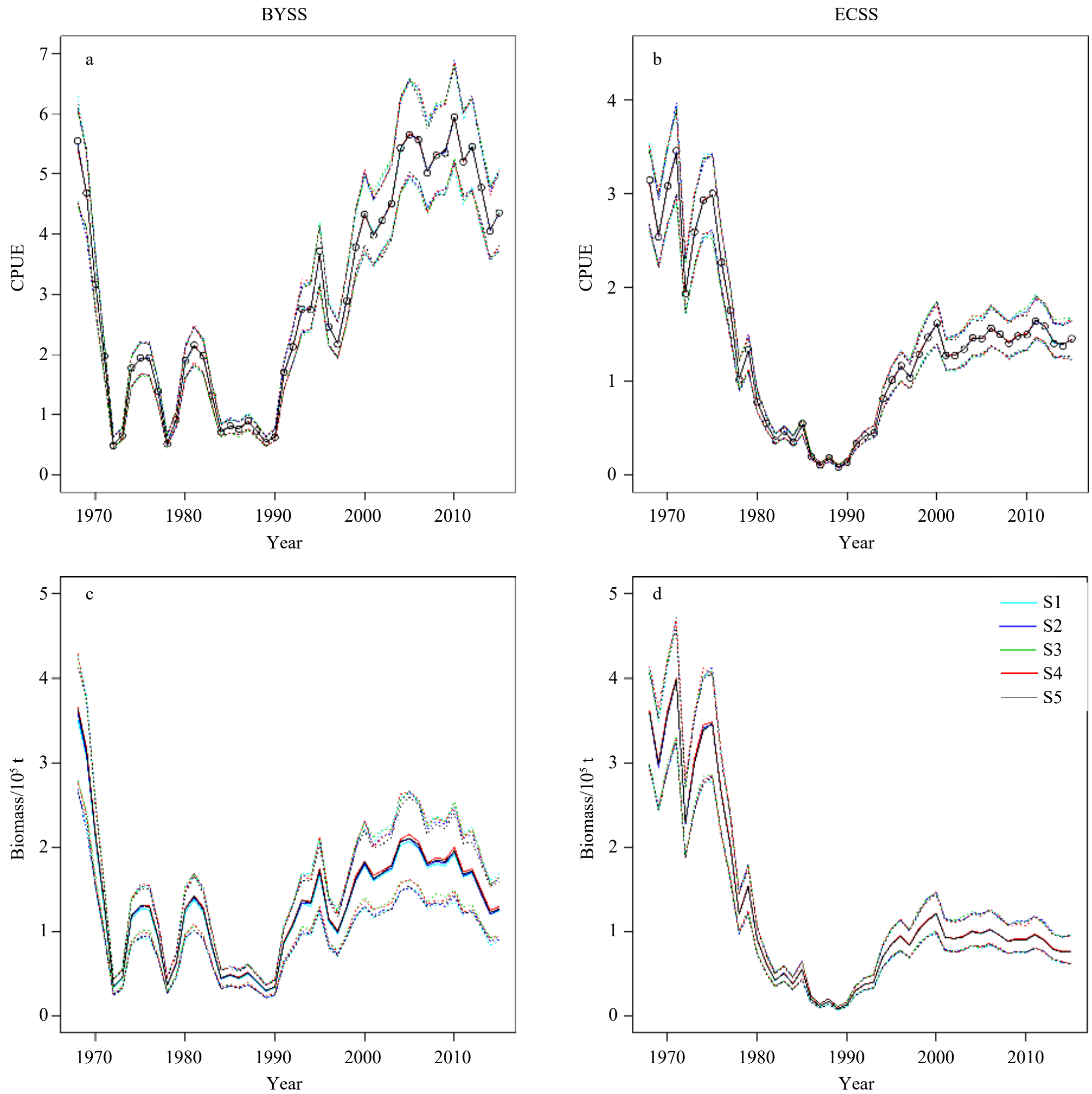

Fig. 8. The estimates of CPUE and biomass for two yellow croaker subpopulations from the subpopulation Model M8. BYSS is the Bohai Sea and Yellow Sea subpopulation, and ECSS the East China Sea subpopulation. Dots represent observation data, solid lines the posterior medians, and dotted lines the 95% credible intervals. Different scenarios (S1–S5) are shown in different colors.

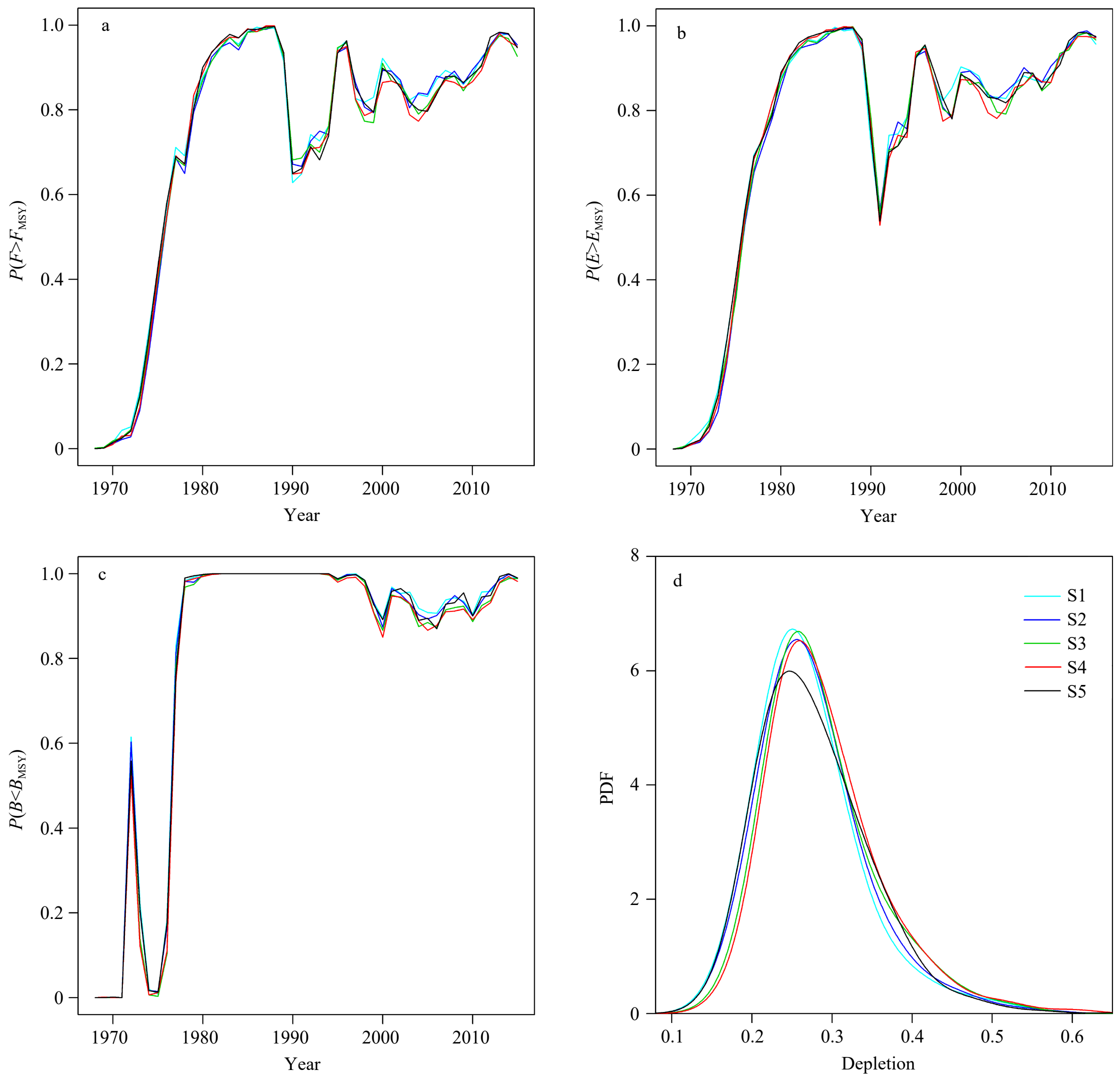

Fig. 9. The probability of fishing mortality being larger than F_{MSY}, i.e., $P(F>F_{MSY})$, the probability of fishing effort being larger than E_{MSY}, i.e., $P(E>E_{MSY})$, the probability of population biomass being smaller than B_{MSY}, i.e., $P(B<B_{MSY})$, and the depletion (biomass in 2015 divided by K) of yellow croaker from Model M4. PDF is the probability density functions. Different scenarios (S1–S5) are shown in different colors.

Table 2. The median and 95% credible intervals for posterior estimations of biological reference points in 2015

Population	Scenario	MSY/10^5 t	B_{MSY}/10^5 t	F_{MSY}	E_{MSY}/10^7 kW	Depletion
Global	S1	4.47(2.30, 8.35)	3.74(2.35, 5.37)	1.24(0.64, 1.90)	1.08(0.59, 1.83)	0.26(0.18, 0.45)
Global	S2	4.28(2.20, 7.40)	3.50(2.28, 5.19)	1.27(0.63, 1.91)	1.07(0.57, 1.74)	0.27(0.18, 0.45)
Global	S3	4.28(2.10, 7.11)	3.36(2.24, 4.76)	1.31(0.63, 1.96)	1.07(0.55, 1.78)	0.27(0.19, 0.45)
Global	S4	4.19(1.98, 7.35)	3.27(2.21, 5.08)	1.31(0.55, 1.94)	1.07(0.52, 1.73)	0.28(0.20, 0.46)
Global	S5	4.29(1.95, 7.62)	3.49(2.29, 5.25)	1.24(0.61, 1.92)	1.07(0.56, 1.73)	0.27(0.18, 0.45)
BYSS	S1	2.00(1.15, 3.03)	1.97(1.51, 2.64)	1.05(0.55, 1.45)	0.28(0.17, 0.44)	0.36(0.26, 0.49)
BYSS	S2	1.97(1.11, 3.19)	2.02(1.49, 2.72)	0.99(0.52, 1.47)	0.28(0.16, 0.44)	0.36(0.26, 0.49)
BYSS	S3	1.97(1.07, 3.13)	2.02(1.51, 2.67)	1.01(0.53, 1.45)	0.29(0.16, 0.45)	0.37(0.28, 0.48)
BYSS	S4	1.99(1.11, 3.10)	2.02(1.56, 2.68)	1.00(0.55, 1.45)	0.29(0.16, 0.45)	0.36(0.27, 0.48)
BYSS	S5	1.97(1.06, 2.91)	1.89(1.48, 2.49)	1.04(0.54, 1.46)	0.28(0.15, 0.43)	0.37(0.27, 0.49)
ECSS	S1	2.37(1.50, 3.33)	2.02(1.65, 2.53)	1.20(0.76, 1.48)	0.65(0.42, 0.85)	0.20(0.15, 0.26)
ECSS	S2	2.43(1.53, 3.28)	2.02(1.68, 2.55)	1.20(0.78, 1.48)	0.67(0.43, 0.88)	0.19(0.15, 0.27)
ECSS	S3	2.38(1.47, 3.40)	2.02(1.64, 2.60)	1.20(0.74, 1.48)	0.67(0.42, 0.88)	0.20(0.14, 0.27)
ECSS	S4	2.40(1.45, 3.40)	2.02(1.59, 2.62)	1.20(0.78, 1.48)	0.67(0.41, 0.87)	0.20(0.15, 0.27)
ECSS	S5	2.39(1.44, 3.34)	1.98(1.64, 2.52)	1.21(0.72, 1.48)	0.67(0.42, 0.87)	0.20(0.15, 0.26)

Note: BYSS is the Bohai Sea and Yellow Sea subpopulation, and ECSS the East China Sea subpopulation.

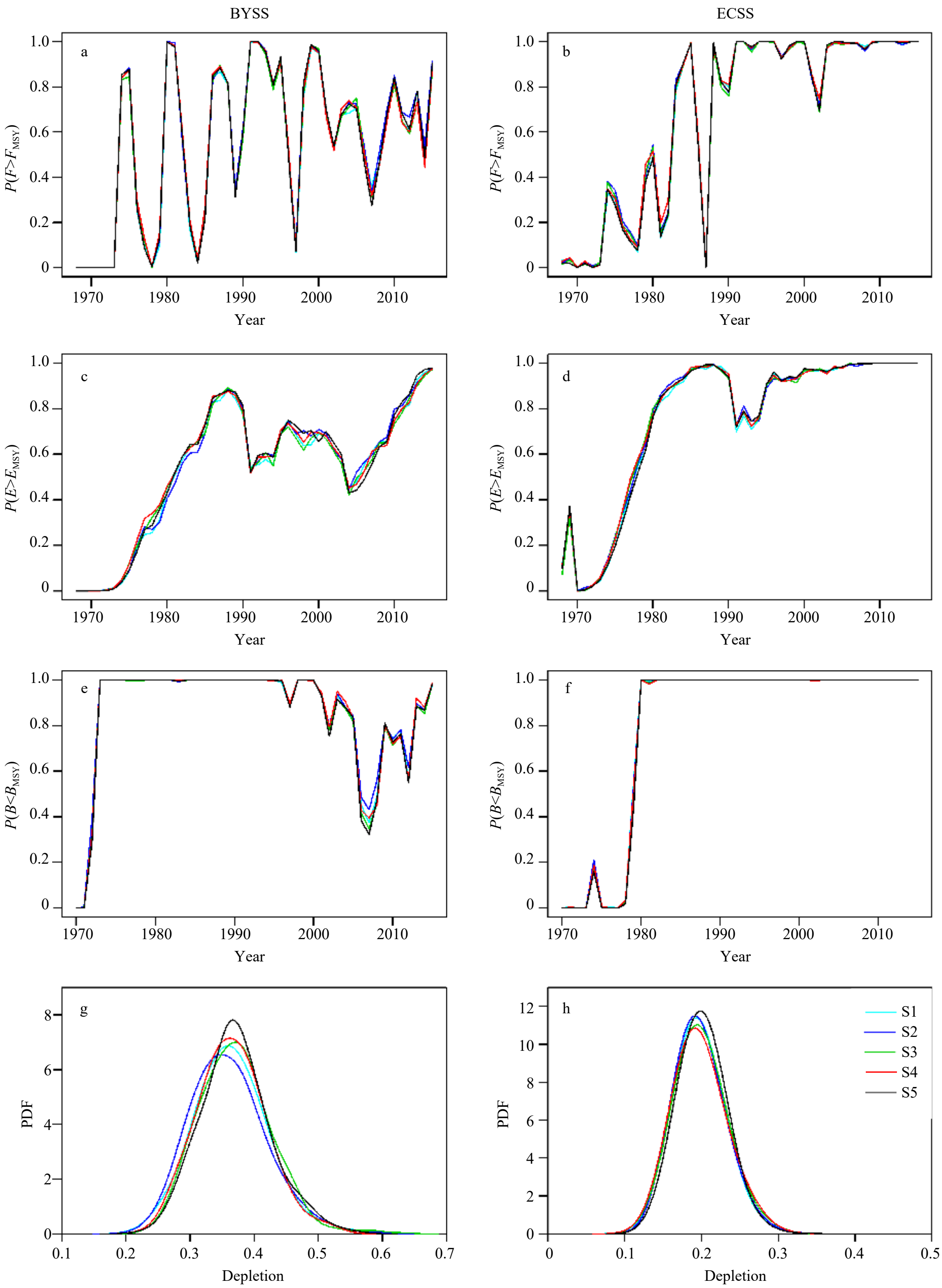

Fig. 10. The probability of fishing mortality being larger than F_{MSY}, i.e., $P(F>F_{MSY})$, the probability of fishing effort being larger than E_{MSY}, i.e., $P(E>E_{MSY})$, the probability of population biomass being smaller than B_{MSY}, i.e., $P(B<B_{MSY})$, and the depletion (biomass in 2015 divided by K) for different yellow croaker subpopulations from the subpopulation Model M8. BYSS is the Bohai Sea and Yellow Sea subpopulation, and ECSS the East China Sea subpopulation. Different scenarios (S1–S5) are shown in different colors.

ulation. Previous studies have shown that individuals of yellow croaker grow faster and mature in their early years. Yellow croaker usually spawns during April and May (Ren et al., 2001), and the younger ones feed and grow faster in summer during the closed fishing season. In recent years, the juvenile yellow croaker of 4 or 5 months old grew to the mean length of 12.75 cm (Cheng et al., 2004), which reached the minimal mesh size of fishing nets. The percentage of the 4- or 5-month-old individuals in the total catch increased from 43% in 1992–1994 to 75% in 2000 (Cheng et al., 2004). Therefore, the population growth rate of yellow croaker has been increasing to high values (even larger than 2). Additionally, the predation mortality on yellow croaker decreased with larger predator fish species being removed by fishing in this region (Matsuda and Abrams, 2006). So the existence of trophic cascade might also have contributed to the increasing growth rate of yellow croaker.

For both the whole population and the subpopulations, the biomass of yellow croaker in 1968 was higher or close to the carrying capacity, which led to the rapid decline of the population size under exploitation. The increased fishing effort led to the continuous depletion of its population. Faced with this situation, the fishery management agency of China began to apply more restrictive strategies, such as Spawning Ground protection program since 1981, introducing Fisheries Law in 1986, and Seasonal Moratorium since mid-1990s (Cao et al., 2017). In this way, the population of yellow croaker began to recover since 1990, and kept relatively stable at a level lower than B_{MSY} in recent years. In the future, further control on fishing effort or overall quota will be needed to recover this population to B_{MSY} level.

The results of the best Bayesian hierarchical models indicated considerable subpopulation variations of yellow croaker population along the coastal areas of China. Before 1990, the biomass of the subpopulation ECSS was much higher than that of the subpopulation BYSS. The conservation management effort has been enhanced to protect fishery resources in China since 1990. Then in 2015, the biomass of the two subpopulations had recovered to two-thirds and one-third of the biomass in 1968 for BYSS and ECSS, respectively. This changes in population size along latitudes might be as a result from global warming. With the increased water temperatures under global warming, the preferred habitat of yellow croaker changed northward, meaning that the northern region becomes its favored habitat, which was also observed for many other aquatic species (Tanaka et al., 2019; Torre et al., 2019). Furthermore, the fishing efforts in the East China Sea was 2.5 times higher than that in the Bohai Sea and Yellow Sea, which might be the other factor that caused geographical variations of yellow croaker subpopulations.

The q estimate for ECSS was much lower than the BYSS. One possible reason is that the fishery targeting yellow croaker of ECSS are from all the south coast provinces, from Jiangsu to Guangdong and Hainan (Bureau of Fisheries and Fishery Administration of Ministry of Agriculture, 1969–2016). For provinces situated far away from the East China Sea, such as Guangdong and Hainan Provinces, would record much lower catchability q. A part of the ECSS is distributed relatively far away from the coast, while BYSS is distributed near the coast, which might lead to the lower q of ECSS.

Apart from the heterogeneity in large spatial scale among two subpopulations of yellow croaker, multiple previous studies have proven the existence of this species local spatial pattern (Lin et al., 2011; Shan et al., 2016; Xiong et al., 2016). The spatial pattern in smaller scale would also influence the population structure and population dynamics of this stock to a degree. Intensive surveys over time with local spatial population distributions are needed for further smaller scale population dynamics analysis (Jiao et al., 2016).

In this study, the values of $P(F>F_{\text{MSY}})$, $P(E>E_{\text{MSY}})$ and $P(B<B_{\text{MSY}})$ were high, almost close to 100%, which indicated unfavorable condition of yellow croaker population in recent years. Additionally, previous studies revealed that smaller sizes at age and earlier maturity might indicate overfishing of yellow croaker over a longer time period (Shan et al., 2016), and the fishing effort has increased 40 times since the 1950s, which contribute to the life history traits shift of yellow croaker (Shan et al., 2013). The status for the two subpopulations was dramatically different, and the risk of overfishing and being overfished for the subpopulation ECSS was higher and increased since 2010, which was consistent with the results of previous studies (Lin, 2004; Li et al., 2011; Liu et al., 2013). Therefore, conservative management strategy was imperative for yellow croaker, especially for the subpopulation ECSS. The biological reference points, estimated from Bayesian models, can be referred to make management strategy for yellow croaker in the future. For instance, the observed fishing effort (0.45×10^7 and 1.26×10^7 kW for BYSS and ECSS, respectively) were much higher than the E_{MSY} (about 0.28×10^7 and 0.67×10^7 kW respectively) for both subpopulations. Therefore, the fishing effort should be controlled more strictly in the fishery management process.

The data used in this study were derived from *China Fishery Statistical Yearbooks* from 1968 to 2015. Fishery data, especially about the fishery dynamics, are essential to conduct stock assessment, and to evaluate and guide sustainable fishery production. *China Fishery Statistical Yearbooks* is the unique fishery-dependent survey data source with high temporal-spatial coverage, which covers all the Chinese coast during these decades. Although there are some controversies about the reliability of this official data (Blomeyer et al., 2012; Campbell and Pauly, 2013; Pauly et al., 2014), there actually has been much researches conducted based on this dataset and yielded valuable knowledge and inferences (Li et al., 2017; Szuwalski et al., 2017; Kang et al., 2018). The official fishery statistics may be with uncertainty but it captured the general trend of the catch and effort, which is much useful to estimate the population dynamics. Additionally, the effort used in this study, power of fishing vessels is considered to be relatively reliable, since during the strict supervision for fishing vessel permit, the power is the important criteria to calculate fuel subsidies that a vessel receives from Chinese government (Kang et al., 2018). Therefore, this study tried the data from this unique and valuable dataset with uncertainties to explore population dynamics by Bayesian model considering different level of errors.

The uncertainty resulted from data collection could be considered to explore its influence for yellow croaker stock assessment. For example, the existence of unregistered vessels could lead to underestimated catch and effort data, which can be tested by complicated sensitivity analysis with different underreporting level. The implementation of zero-growth strategy for total catch of marine fishery in 1999 and negative-growth strategy in 2000, could influence the fishery dynamics and might increase the bias of the estimated population dynamics. Additionally, the fishery dependent data are not available from Korean fishery, in which BYSS of yellow croaker has been one target species. The catchability, fishing season and ground are different among Chinese and Korean fishery, leading to some stock assessment uncertainty. Therefore, much more efforts are required to improve the fishery monitoring program and to consider the uncertainty of data for stock assessment in future studies.

5 Conclusions

The population dynamics modelling in this study revealed that the population growth rate of yellow croaker and its fishery catchability along the coast of China exhibit increasing pattern, which are likely due to the evolutionary response of the population facing intensive fishing and the improvement in catching technique separately. The biomass of yellow croaker depleted and recovered to a relatively stable level with spatial heterogeneity, but this important fishery is still overfished and subject to overfishing in recent years. Consequently, more conservative management strategy based on the biological reference points from the population dynamics models was imperative for yellow croaker along the coast of China, considering the heterogeneity of two subpopulations (BYSS and ECSS).

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