
Errata

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In search of climate effects on Atlantic Croaker (*Micropogonias undulatus*) stock off the U.S. Atlantic coast with Bayesian state-space biomass dynamic models

Corrections:

On page 56, Equation 6 is missing an equal sign in the calculation of the deviance statistic D . The equation should read as follows:

$$D(\Theta) = -2\log L(\Theta) = -2\log[P(O|\Theta)]$$

On page 70, the age symbol in Equation A2 should be a , instead of α (alpha). Equation A2 should read as follows:

$$F_a = \beta \{L_\infty [1 - \exp(-K(a - a_0))]\}^\gamma$$

Abstract—Atlantic Croaker (*Micropogonias undulatus*) production dynamics along the U.S. Atlantic coast are regulated by fishing and winter water temperature. Stakeholders for this resource have recommended investigating the effects of climate covariates in assessment models. This study used state-space biomass dynamic models without (model 1) and with (model 2) the minimum winter estuarine temperature (MWET) to examine MWET effects on Atlantic Croaker population dynamics during 1972–2008. In model 2, MWET was introduced into the intrinsic rate of population increase (r). For both models, a prior probability distribution (prior) was constructed for r or a scaling parameter (r_0); inputs were the fishery removals, and fall biomass indices developed by using data from the Multispecies Bottom Trawl Survey of the Northeast Fisheries Science Center, National Marine Fisheries Service, and the Coastal Trawl Survey of the Southeast Area Monitoring and Assessment Program. Model sensitivity runs incorporated a uniform(0.01,1.5) prior for r or r_0 and bycatch data from the shrimp-trawl fishery. All model variants produced similar results and therefore supported the conclusion of low risk of overfishing for the Atlantic Croaker stock in the 2000s. However, the data statistically supported only model 1 and its configuration that included the shrimp-trawl fishery bycatch. The process errors of these models showed slightly positive and significant correlations with MWET, indicating that warmer winters would enhance Atlantic Croaker biomass production. Inconclusive, somewhat conflicting results indicate that biomass dynamic models should not integrate MWET, pending, perhaps, accumulation of longer time series of the variables controlling the production dynamics of Atlantic Croaker, preferably including winter-induced estimates of Atlantic Croaker kills.

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In search of climate effects on Atlantic Croaker (*Micropogonias undulatus*) stock off the U.S. Atlantic coast with Bayesian state-space biomass dynamic models

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The Atlantic Croaker (*Micropogonias undulatus*) is a demersal sciaenid species common in estuarine and coastal waters of the U.S. Atlantic coast (Chao and Musick, 1977). This species is abundant off the U.S. mid- and southeast Atlantic coast, where it forms a single genetic population and management stock-unit supporting important commercial and recreational fisheries (Atlantic States Marine Fisheries Commission [ASMFC]¹). Exploitation of Atlantic Croaker began in the 1800s, but coastwide (New Jersey–east Florida) commercial removals and bycatch estimates have been consistently reported only since 1950 and recreational harvests and catches since 1981. These statistics show periodic, sudden highs and lows over the time series (Fig. 1A).

Although fishing can have a significant impact on the Atlantic Croaker population (ASMFC¹; Hare et al., 2010), Hare and Able (2007) advocated the hypothesis that population “outbursts” and harvest variability of Atlantic Croaker are largely driven by long-term trends in winter tem-

perature. This idea was consistent with the observations that juvenile (age-0) Atlantic Croaker spend their first winter (December–March) in estuarine nursery habitats where winter water temperatures appear to regulate juvenile Atlantic Croaker survival and year-class strength (Norcross and Austin;² Lankford and Targett, 2001a, 2001b; Hare and Able, 2007; Hare et al., 2010). The mechanistic link between abundance of juvenile Atlantic Croaker and water temperature led Hare and Able (2007) to develop a conceptual model in which sequential warm winters result in high juvenile survival rates. Such high rates of juvenile survival would in turn lead to large year-classes that increase the population size. The reverse would be true of cold winters. These authors found positive, often significant correlations between spring juvenile and adult (age-2) abundances and minimum winter estuarine temperature (MWET) and between coastwide adult catch and either MWET or the North Atlantic Oscillation.

¹ ASMFC (Atlantic States Marine Fisheries Commission). 2010. Atlantic Croaker 2010 benchmark stock assessment. ASMFC, Washington, D.C., 336 p. [Available from <http://www.sefsc.noaa.gov/sedar/download/Atlantic%20Croaker%20Stock%20Assessment%20Report.pdf?id=DOCUMENT>, accessed January 2012.]

² Norcross, B.L., and H.M. Austin. 1981. Climate scale environmental factors affecting year class fluctuations of Chesapeake Bay croaker, *Micropogonias undulatus*. Special Scientific Report 110, 78 p. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. [Available from <http://web.vims.edu/GreyLit/VIMS/ssr110.pdf>.]

Their results supported a hypothesis put forward by Joseph (1972) and concurred with the findings of Norcross and Austin.² Joseph (1972) analyzed the fluctuations of commercial landings for Atlantic Croaker from the Mid-Atlantic Bight (1890–1967) and discussed 4 possible causes of their sudden decline after 1945 (i.e., recruitment overfishing, habitat degradation by humans, multispecies interactions, and environmental forcing due to natural events). He dismissed the first three causes as potential driving forces of the declining landings and attributed that decline to extremely low winter temperatures that had decimated overwintering age-0 Atlantic Croaker in estuarine nursery habitats. He documented evidence that large landings had been associated with warming of sea temperatures and that the historical declines in landings had always followed cooling trends. On the basis of this information, he originally proposed the overwintering mortality hypothesis in juvenile Atlantic Croaker during cold winters, resulting in weak year-classes and future, low population sizes.

This hypothesis has been repeatedly adopted in subsequent studies. In this respect, Norcross and Austin² showed that the abundance of juvenile Atlantic Croaker in Chesapeake Bay (Virginia) during summer positively correlated with estuarine water temperature during the previous winter. They associated the increase in catch in the mid-1970s with warmer winter temperatures and a decrease in catch in the late-1970s with colder winter temperatures.

With the exception of the study by Hare et al. (2010), studies of the population dynamics and management of Atlantic Croaker have ignored environmental effects on the processes modeled (Barbieri et al., 1997; Lee, 2005; ASMFC^{3,1}). On the basis of a mechanistic recruitment–winter temperature hypothesis (described above), Hare et al. (2010) developed a coupled climate–population dynamics model. This model is an age-structured production model in which recruitment is generated through a stock-recruit relation, and the age composition is simulated to be conditional on the closest correspondence between predicted and observed harvests. The climate effects are log-linearly incorporated into the model through a Ricker spawning-stock function with a temperature (i.e., MWET) variable. The coupled model indicates that both exploitation and climate changes significantly affect Atlantic Croaker abundance. Importantly, Hare et al. (2010) found a significant correlation between the observed Atlantic Croaker recruitment and MWET, which thereby supports the mechanistic recruitment hypothesis of Hare and Able (2007).

The Atlantic Croaker stock in U.S. Atlantic waters can be considered data-moderate. In fact, this stock has

been associated with many data sets, some of which were characterized by considerable uncertainty in their estimates and representativeness. For example, the ASMFC stock assessment subcommittees (ASMFC^{3,1}) identified numerous small-scale (i.e., bay- or sound-specific) and 2 large-scale (i.e., spanning wide areas, many years, or both) survey indices of abundance, one coastwide or regional fishery-dependent index (i.e., the total catch per unit of effort [CPUE] from the National Marine Fisheries Service [NMFS] Marine Recreational Fisheries Statistics Surveys [MRFSS]), and various sources of fish kills and length data.

Evaluation of these data sets and assessment procedures revealed the following. The small-scale indices of abundance possibly reflected better local than coastwide dynamics. The first stock assessment (ASMFC³) lacked catch-at-age (CAA) data and dealt with conflicting trends in regional indices of abundance. The southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) bycatch, commercial fishery discards, and scrap (or bait) fishery landings are currently considered significant but have been poorly characterized. The development of the MRFSS CPUE appeared unreliable and raised concerns about its value as relative index of stock abundance (ASMFC¹). In this context, differing decisions and assessment choices have been adopted. Preference has been given to large-scale survey indices and, in order to characterize recruitment, to a few small-scale indices developed from survey data collected in the so-called overwintering core area for juveniles. The first stock assessment of Atlantic Croaker (ASMFC³) relied on an age-structured production model (1973–2002).

Because of the difficulties encountered in reconciling the conflicts between regional indices, regional models have been developed, thereby splitting the stock into the “northern” and “southern” management units. The model for the south Atlantic region, however, did not perform satisfactorily. Because that portion of the stock could not be assessed, emphasis was placed on the “northern” stock. In contrast, the 2010 assessment subcommittee (ASMFC¹) did not find evidence to support a north–south separation of the stock and conducted an assessment encompassing data for the coastwide stock. Moreover, this subcommittee developed matrices of CAA for 1988–2008 only and explored various assessment approaches, including continuity runs, but ultimately chose a statistical CAA model that uses the aforementioned CAA data.

The results of that model form the basis for current management. Unfortunately, inadequate estimates of the SESTF bycatch and scrap fishery landings particularly hampered the determination of overfished status of the stock. Meanwhile, various ASMFC stock-assessment subcommittees and review panels documented information about climate effects on the population dynamics of Atlantic Croaker. They consequently recommended that stock assessment models investigate environmental covariates to improve understanding of the

³ ASMFC (Atlantic States Marine Fisheries Commission). 2005. Atlantic Croaker stock assessment and peer review reports. ASMFC, Washington, D.C., 370 p. [Available from <http://www.asmf.org/>, accessed January 2012.]

dynamics in question and management implications. Hare et al.'s (2010) work provides guidance, serving as a preliminary study with respect to the recommendation for age-structured models.

The primary purpose of this study was to investigate whether biomass dynamic models (BDMs) could capture the MWET effects on the population dynamics of Atlantic Croaker off the U.S. Atlantic coast and to determine how this result effected the status determination of the stock. Use of BDMs was aimed to address ASMFC's need and Hare et al.'s (2010, p. 461) suggestion regarding exploration of alternative models incorporating MWET, given that BDMs have the potential to track environmental perturbations (Keyl and Wolff, 2008). Unlike Hare et al. (2010), who dealt only with the "northern" stock of Atlantic Croaker, consistent with ASMFC,³ BDMs here incorporated relevant data for the coastwide stock in accordance with ASMFC.¹ Analyses relied upon a Bayesian state-space modeling framework with software from the Bayesian inference Using Gibbs Sampling (BUGS) Project.

The influence of MWET on Atlantic Croaker stock biomass and productivity was investigated by two complementary approaches. First, process errors were introduced into a traditional BDM so that it could be determined whether those errors reflected environmental anomalies, assumed here to be largely dominated by changes in winter estuarine temperature (Joseph, 1972; Hare and Able, 2007; Hare et al., 2010) and, hence, showed some relationship with MWET. Second, we investigated the effects of explicitly incorporating MWET into a BDM—that would yield effects on both population dynamics and management parameters.

Materials and methods

Data

This study relied on fishery and survey data used in ASMFC¹ BDMs, except for the MRFSS CPUE because its development was questionable and because it was not considered a reliable index for stock biomass. The fishery-dependent removals (Fig. 1A) included 1) coastwide aggregates of commercial fishery landings and commercial finfish bycatch and discards (1972–2008), 2) coastwide recreational kills (1981–2008), 3) North Carolina scrap landings (1981–2008), and 4) SESTF bycatch (1972–2008).

The NMFS, the Atlantic Coastal Cooperative Statistics Program, and individual state fishery agencies have participated in collecting commercial landings data using various temporal resolutions and reporting requirements and processes. Reported commercial landings for all gear types (including the landed SESTF bycatch) were obtained from the Atlantic Coastal Cooperative Statistics Program Data Warehouse and, in 3 cases, from individual state reports. The commercial finfish bycatch or discards were estimated for gill nets

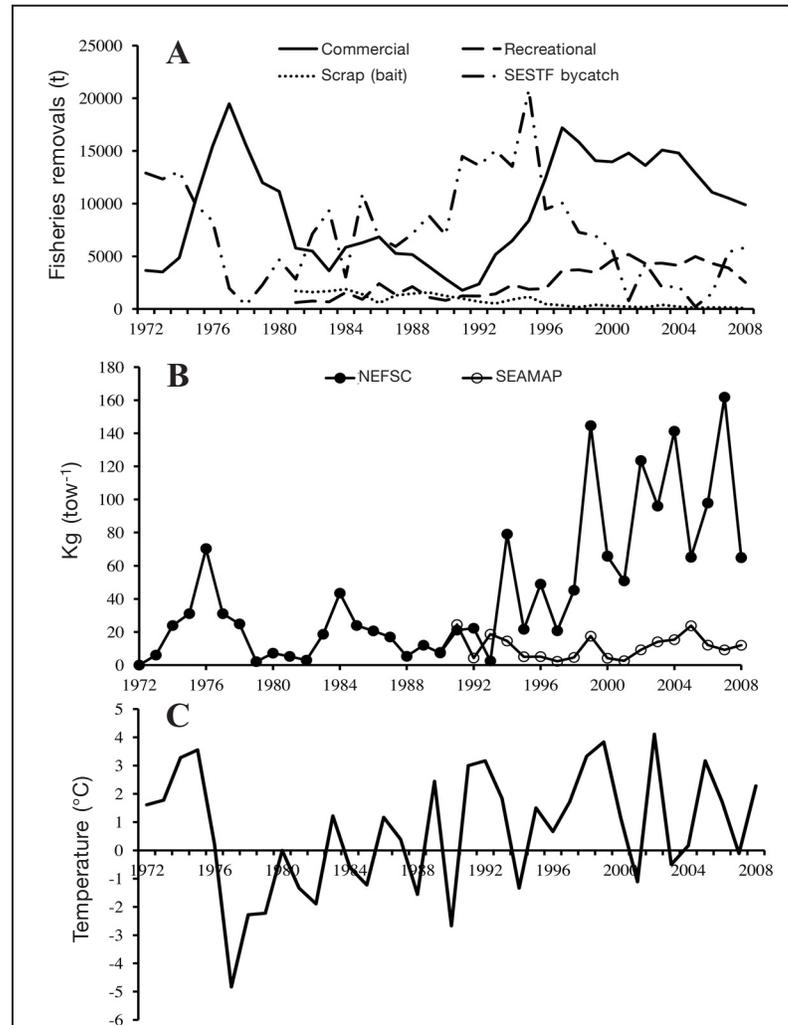


Figure 1

Time series for the period of 1972–2008 of (A) commercial, recreational, and scrap (bait) fishery removals and bycatch of the southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) for Atlantic Croaker inhabiting the U.S. Atlantic coast; (B) biomass indices for Atlantic Croaker inhabiting the U.S. Atlantic coast, specifically the National Marine Fisheries Service–Northeast Fisheries Science Center (NEFSC) fall index and the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index; and (C) winter air temperature for Virginia as a proxy for minimum winter estuarine temperature.

and otter trawls by using the geometric mean of the ratios of observed discards to reported landings. These ratios were developed from the NMFS Observer Program data set.

The recreational kills consisted of type A (dead fish brought ashore and available for identification by interviewers), type B1 (fish not brought ashore, hence not seen by samplers, but were used as bait or were discarded dead), and type B2 (fish released alive; they were of small sizes, with a 10% assumed release mortality). They were obtained from data-collection programs operated by the NMFS MRFSS since 1981. Estimates of North Carolina scrap fishery landings were provided by the North Carolina Division of Marine Fisheries, which is the only state agency that routinely sampled such a fishery since 1986 (the 1981–85 estimates were based on the proportion of Atlantic Croaker in the unclassified finfish bait landings during 1986–90).

Atlantic Croaker also are one of the major components of the SESTF bycatch, but the magnitude of the SESTF Atlantic Croaker discards is highly uncertain. The related estimates were produced by using a simple fish-catch to shrimp-catch ratio for study materials collected in North Carolina and South Carolina, and the resulting catch ratio was expanded to the entire coast. Such estimates largely exceeded the reported landings in most years (Fig. 1A) but were considered extremely crude and unreliable. For this reason, ASMFC¹ omitted the SESTF bycatch in BDMs and included them in the age-structured model for sensitivity runs only. Likewise, the SESTF bycatch estimates were used here for sensitivity analyses.

Biomass indices (Fig. 1B) included the fall (September–November) components of the Multispecies Bottom Trawl Survey (1972–2008) of the NMFS Northeast Fisheries Science Center (NEFSC) and the Coastal Trawl Survey (1990–2008) of the multiagency Southeast Area Monitoring and Assessment Program (SEAMAP). The NEFSC and SEAMAP indices were chosen because the corresponding surveys showed wide geographic coverage, temporal coverage, or both; have been conducted consistently; and have provided evidence of regular encounters with Atlantic Croaker of different age groups (ASMFC¹ Appendix 1). Moreover, unlike the coastwide MRFSS CPUE, the NEFSC and SEAMAP indices were considered reflective of the Atlantic Croaker stock size and trajectory (ASMFC¹). Although various model runs used the MRFSS CPUE during the 2010 stock assessment, this index raised many concerns and therefore it was excluded from the final assessment model (ASMFC¹).

MWET was added as a variable of environmental forcing of the Atlantic Croaker population dynamics. Winter air temperature data for Virginia—a Chesapeake Bay region state—were extracted from the website of the Southeast Regional Climate Center (http://www.sercc.com/climateinfo_files/monthly/Virginia_temp.html, accessed May 2012). Air temperature is considered a good proxy for estuarine water temper-

ature because of the efficient ocean-atmosphere heat exchange in estuarine systems (Hare and Able, 2007). On the U.S. Atlantic coast, winter temperatures of one location (here, the Chesapeake Bay region) are a good proxy for the entire coast owing to a strong coherence among local winter temperatures (Joyce, 2002; Hare et al., 2010). As shown in Hare and Able (2007) and Hare et al. (2010), MWET corresponded with the minimum monthly mean air temperature from December to March. Specifically, MWET values were the mean temperatures of the coldest months during the winter seasons. The Chesapeake Bay region's MWET (Fig. 1C) was suited for a study of its effects on the Atlantic Croaker population dynamics because the Chesapeake Bay region is a major overwintering nursery area for the species (Hare et al., 2010).

Biomass dynamic models

The analyses covered the 1972–2008 period, consistent with the years for which data for BDM implementations were available in the 2010 stock assessment (ASMFC¹). Two Bayesian state-space biomass dynamic models (BSSBDMs) were developed and used: a discrete BSSBDM without MWET (model 1, M1) and a discrete BSSBDM that integrated MWET (model 2, M2). Both models used a one-year time (t) step. A state-space model describes 2 interrelated time series of state and observation processes (Buckland et al., 2004), both of which account for random errors. The state process defined the stochastic temporal dynamics of the unobserved (or latent) age-aggregated stock size of Atlantic Croaker that is due to natural variation. The corresponding error, referred to as process error, is the joint effect of random multiplicative factors (e.g., fluctuations in life history parameters, trophic interactions, environmental disturbance). The process error in M1 included all forms of environmental variations and, in M2, environmental variations over and above the variations pertaining to MWET. The observation errors (arising from measurement and sampling errors) related only to observed indices of biomass. These indices were assumed to be a linear function of the latent biomass.

Consistent with Meyer and Millar (1999) and Millar and Meyer (2000), M1 and M2 described the processes under consideration through a set of 3 probability density functions (PDFs) $g(\cdot)$ and $h(\cdot)$, given the latent, beginning-of-the-year exploitable biomass (B_t), the sets of unknown model parameters (Θ), the set of known covariates (C), and observed indices of biomass by year (O_{it} ; i = NEFSC index, SEAMAP index):

$$g_{1972}(B_{1972} | \Theta)$$

Initial (1972) state PDF (1a)

$$g_t(B_{t+1} | B_t, \Theta, C)$$

State PDF ($t = 1973, \dots, 2008$) (1b)

$$h_{it}(O_{it} | B_t, \Theta)$$

$$\begin{aligned} & \text{Observation process PDF} \\ & (i = 1, \dots, 2; t = 1972, \dots, 2008). \end{aligned} \quad (1c)$$

Specifically, $\mathbf{C} = \mathbf{R} \cup \mathbf{W}$; $\mathbf{R} = \{R_t\}$, the set of total fishery removals ($t=1972, \dots, 2008$); and $\mathbf{W} = \{W_t\}$, the set of MWET time series ($t= 972, \dots, 2008$). For M1, B_t was exposed only to fishing ($\mathbf{C} = \mathbf{R}$). For M2, B_t was affected by both fishing and water winter temperature ($\mathbf{C} = \mathbf{R} \cup \mathbf{W}$). For simplicity, the fisheries removals were assumed to be known perfectly. The SEAMAP index during 1972–89 was treated as an unobserved random variable because it was unavailable across that period.

The deterministic, time-discrete part of biomass expectation in M1 and M2 is expressed as

$$E(B_{t+1}) = \hat{B}_{t+1} = B_t + G_t - \sum_f R_{ft}, \quad (2)$$

where f = a subscript for fishery and, during year t ;
 G_t = production that quantifies the overall change in biomass due to somatic growth, recruitment, and natural mortality; and
 R_{ft} = fishery-specific removals.

G_t is a function of B_t , the intrinsic rate of population increase (r), and the carrying capacity (B_∞). The Graham-Schaefer (or logistic) form was chosen to quantify G_t because of its simplicity (it has 2 parameters, r and B_∞) and because it is a central case among possible shapes of production models (Prager, 1994). Therefore, for M1,

$$G_t = rB_t \left(1 - \frac{B_t}{B_\infty} \right). \quad (3a)$$

In biomass dynamic modeling with environmental effects, environmental factors can act on the stock productivity (i.e., on r , B_∞ , or both), the fisheries' or surveys' catchabilities, or both (Fréon, 1988; Jacobson et al., 2005; Jensen, 2002, 2005). MWET was normalized and introduced into the parameter r because MWET affects Atlantic Croaker productivity through growth or recruitment during the prerecruit stage (Hare and Able, 2007). The approach followed the framework of log-linearly adding environmental covariates into fisheries models (e.g., Hilborn and Walters, 1992) and assuming implicit controlling effects of MWET on recruitment (Iles and Beverton, 1998; Levi et al., 2003). Therefore, for M2, the year-specific intrinsic rate of increase (r_t) is

$$r_t = r_0 e^{\alpha W_t}, \quad (3b)$$

where α is a coefficient controlling (linearly) the influence of MWET on Atlantic Croaker productivity and r_0 is a scaling parameter. In common with similar applications (e.g., Maunder and Watters, 2003), α was limited to values greater than zero because MWET is positively correlated with juvenile production (Norcross and Austin²; Hare and Able, 2007).

To improve the efficiency of the Markov Chain Monte Carlo (MCMC) estimation algorithm implemented

in BUGS, the state-space formulations of M1 and M2 were expressed in terms of depletions, b_t ($b_t = B_t/B_\infty$), herein considered to be “true” and assumed to have log-normal distributions (Meyer and Millar, 1999; Millar and Meyer, 2000):

$$\begin{aligned} b_{1972} & \sim LN \left[\log(\hat{b}_{1972}), \tau_p^2 \right] \\ & \text{for M1 and M2,} \end{aligned} \quad (4a)$$

$$\begin{aligned} b_{t+1} & \sim LN \left\{ \log \left[(1+r)\hat{b}_t - r b_t^2 - b_\infty \sum_f R_{ft} \right], \tau_p^2 \right\} \\ & \text{for M1 } (t = 1973, \dots, 2008),^4 \end{aligned} \quad (4b)$$

$$\begin{aligned} b_{t+1} & \sim LN \left\{ \log \left[(1+r_t)\hat{b}_t - r_t b_t^2 - b_\infty \sum_f R_{ft} \right], \tau_p^2 \right\} \\ & \text{for M2 } (t = 1973, \dots, 2008), \end{aligned} \quad (4c)$$

where \hat{b}_t = the expected depletion in year t , treated as deterministic;

$b_\infty = 1/B_\infty$; and

τ_p^2 = the precision (inverse of the variance, σ_p^2) of the process error.

For the observation error model (Eq. 1c), each biomass index (i_{ij}) was assumed to be proportional to the year- and period (j)-specific biomass and to be log-normally distributed about its expected, model estimate (\hat{i}_{ij}):

$$i_{ij} \sim LN \left[\log(\hat{i}_{ij}), \tau_{ij}^2 \right] \quad (5a)^5$$

$$\hat{i}_{ij} = A_{ij} \Phi_1 b_t B_\infty. \quad (5b)$$

For the NEFSC index, $j=1$ (1972–93) when the index varied at low levels with no obvious trend or 2 (1994–2008) when the index showed an overall increasing trend (Fig. 1B). In fact, this index indicates that Atlantic Croaker accessibility and vulnerability changed between these periods. For the SEAMAP index, $j = 1$ (1990–2008) because the index varied without trend (Fig. 1B). In Equation 5a,

τ_{ij}^2 = the observation error precision ($\tau_{ij}^2 = 1/\sigma_{ij}^2$, σ_{ij}^2 is the observation error variance) by period.

In Equation 5b,

⁴ Equation 4 a–c corresponds with BUGS parameterizations and code. The usual stochastic formulation of Equation 4b, for example, is $b_{t+1} = \left[(1+r)\hat{b}_t - r b_t^2 - b_\infty \sum_f R_{ft} \right] e^{\varepsilon_t}$,

where $\varepsilon_t \sim N(0, \sigma_p^2)$ and $(1+r)\hat{b}_t - r b_t^2 - b_\infty \sum_f R_{ft} = \hat{b}_{t+1}$. The expected (deterministic) biomass (\hat{B}_{t+1}) and the stochastic (true) biomass (B_{t+1}) in year $t+1$ are $\hat{B}_{t+1} = \hat{b}_{t+1} B_\infty$ and $B_{t+1} = b_{t+1} B_\infty = \hat{b}_{t+1} B_\infty e^{\varepsilon_t}$. The same formulation applies for Equation 4, a and c.

⁵ The usual stochastic formulation of Equation 5a is $i_{ij} = \hat{i}_{ij} e^{\omega_{ijt}}$, with $\omega_{ijt} \sim N(0, \sigma_{ij}^2)$.

- A_{ij} = the stock availability coefficient by period, assumed to reflect all biological and ecological factors affecting the stock;
- Φ_i = the survey's global efficiency, assumed to be constant and to measure human and technological factors of the survey while catching animals available in the sampled strata.

The assumption of constant Φ_i implies a time-invariant sampling protocol, which has broadly prevailed for each survey program during the time frame considered. Both A_{ij} and Φ_i modify the survey catchability by period (q_{ij}), which was expressed as $q_{ij} = A_{ij}\Phi_i$. Note that, for each survey, q ranges from zero to one; in other words, $A \in [0,1]$ and $\Phi \in [0,1]$; $q = 0$ if $A = 0$ (unavailable animals during the survey) or $\Phi = 0$ (inefficient survey).

Model parameters, derived quantities, and parameter estimation procedure

The sets of parameters were $\Theta = \{r, b_\infty, \sigma_p^2, \sigma_{ij}^2, A_{ij}, \Phi_i, \hat{b}_{1972}\}$ for M1 and $\Theta = \{r_0, \alpha, b_\infty, \sigma_p^2, \sigma_{ij}^2, A_{ij}, \Phi_i, \hat{b}_{1972}\}$ for M2. The derived metrics included $b_{1972}, \dots, b_{2008}$; B_∞ ; $B_{1972}, \dots, B_{2008}$ (assumed to follow a lognormal distribution); $SEAMP_{1972}, \dots, SEAMP_{1989}$; q_{ij} ; the expected maximum sustainable yield, \overline{MSY} ($\overline{MSY} = rB_\infty/4$); the expected biomass and harvest rate at \overline{MSY} ($\hat{B}_{MSY} = B_\infty/2$ and $\hat{H}_{MSY} = r/2$); the biomass and fishery-specific harvest ratios B_t/\hat{B}_{MSY} and H_t/\hat{H}_{MSY} ; and for M2, $r_{1972}, \dots, r_{2008}$. The previous metrics for management strictly relate to M1. For M2, $\hat{B}_{MSY} = B_\infty/2$ and the ratio B_t/\hat{B}_{MSY} are still valid, but other metrics are year-specific (Fréon, 1988; for comparable alternatives, see Jacobson et al., 2005; Jensen, 2005) and *de facto* log-linearly related to MWET: $\overline{MSY}_t = r_t B_\infty/4$, $\hat{H}_{MSY}_t = r_t/2$, and the harvest ratio is H_t/\hat{H}_{MSY}_t . Each fishery-specific harvest rate was estimated as $H_t = R_t/B_t$. The total harvest rates and harvest ratios were calculated similarly, across fisheries.

The BSSBDM parameters were assumed to be mutually independent. The Bayes theorem (e.g., Hilborn and Mangel, 1997) was used to estimate the posterior distributions of the BSSBDM parameters and of the derived metrics or statistics of interest. The use of the Bayes theorem first required specification of prior PDFs, $P(\Theta)$, about knowledge or hypotheses on Θ (Table 1), independent of information contained in biomass indices. The models were then fitted to the observed data of biomass indices (O) by using a likelihood (or sampling density) function, $L(\Theta) = P(O|\Theta)$ and, in the process, updated $P(\Theta)$ into the joint posterior probability, $P(\Theta|O)$.

A prior PDF was developed for the parameter r only (Appendix 2) on the basis of Atlantic Croaker demographics (Appendix 3). This PDF was applied to both M1 and M2 but stood for r_0 in M2 (Table 1). To aid direct comparison of models, priors for other parameters were specified similarly with noninformative distributions (here gamma, uniform, or normal; henceforth

denoted G , U , and N , respectively). Similar to the role played by b_∞ in lieu of B_∞ , priors were assigned to $a_{ij} = 1/A_{ij}$ and $\varphi_i = 1/\Phi_i$ to increase the mixing speed and efficiency of the Gibbs sampler underlying BUGS; A_{ij} and Φ_i were derived *a posteriori*. The choice of noninformative priors (Table 1) was dictated by ignorance of most parameters, but those priors have been constrained to fall within bounds suspected to give support to plausible parameter values. For example, B_∞ was assumed to be uniformly distributed between 10× and 100× the observed total fishery removals.

The Gibbs sampler, a MCMC, numerically intensive technique implemented in the WinBUGS software (vers. 1.4.3;⁶ Lunn et al., 2000), was used to sample parameter vectors from the joint posterior distributions. WinBUGS was run, without starting values, from R software (vers. 2.15.3; R Development Core Team, 2013) by employing the package R2WinBUGS (Sturtz et al., 2005).

The key issue in MCMC simulations is determination of when the chain has adequately converged (i.e., when the random draws, also called samples, or iterations, truly represent the posterior distribution). In theory, convergence occurs when the number of iterations increases to infinity, but an infinite number of iterations poses problems of computer storage and computing time. Moreover, MCMC samples are characterized by autocorrelation of initial values within the chain. In practice and by convention, convergence can be achieved by lengthening the chain, autocorrelation can be reduced by discarding some initial draws (the burn-in period), and disk space is preserved by keeping one draw every several iterations (thinning). The burn-in period and the thinning interval also must be long.

In this study, 3 independent chains, each with 100,000 iterations, a burn-in period of 50,000 draws, and a thinning interval of 10 (1 in every 10 values was kept) were simulated and led to satisfying convergence diagnostics. Therefore, 5000 iterations for each chain were saved and used for inference. Convergence of MCMC simulations to posterior distributions was checked by inspecting the traces, autocorrelation plots, and Gelman-Rubin (G-R) statistic. In R2WinBUGS, the G-R statistic is called a potential scale-reduction factor or \hat{R} statistic; at convergence, $\hat{R} \approx 1$, 1.1 being an acceptable threshold (Sturtz et al., 2005). This statistic is considered sufficient in most practical situations (Rivot et al., 2004). The final marginal posterior PDFs were summarized in terms of the mean, standard deviation, median, and the 2.5th and 97.5th percentiles, which define the 95% Bayesian central interval (95% BCI). A 95% BCI means that there is exactly a 0.95 probability that the true value of a parameter lies within that interval given the model, data, and priors (Ellison, 2004; Grobois et al., 2008; Kéry, 2010).

⁶ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Specifications of the probability density functions (PDFs) of priors for parameters implemented in Bayesian state-space biomass dynamic models: without minimum winter estuarine temperature, MWET(model 1, M1), and with MWET (model 2, M2) for Atlantic Croaker off the U.S. Atlantic coast, 1972–2008. The lognormal, gamma, and uniform prior PDFs are symbolized by LN , G , and U , respectively. Priors are vague except for the parameter r (M1) or the parameter r_0 (M2). Tuning indices were the National Marine Fisheries Service–Northeast Fisheries Science Center (NEFSC) fall index and the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index.

Parameter	Definition	PDFs of priors for M1 or M2
r	Intrinsic growth rate	$LN(-0.756, 0.0086)^1$
r_0	Scale factor of the intrinsic growth rate	$LN(-0.756, 0.0086)^{1,2}$
α	Coefficient of the linear effect of MWET	$G(0.01, 0.001)^2$
b_∞	Inverse of carrying capacity (B_∞)	$U(0.0000005, 0.000005)$
σ_p^2	Process error variance	$U(0.0000004, 0.000004)^3$
$\sigma_{NEFSC72-93}^2$	Observation error variance for NEFSC index, 1972–1993	$G(0.01, 0.001)$
$\sigma_{NEFSC94-08}^2$	Observation error variance for NEFSC index, 1994–2008	$U(0.01, 1)$
σ_{SEAMAP}^2	Observation error variance for SEAMAP index, 1990–2008	$U(0.01, 1)$
$\alpha_{NEFSC72-93}$	Inverse of the stock availability coefficient inferred from NEFSC index ($A_{NEFSC72-93}$), 1972–93	$U(0.01, 10)$
$\alpha_{NEFSC94-08}$	Inverse of the stock availability coefficient inferred from NEFSC index ($A_{NEFSC94-08}$), 1994–2008	$U(0.01, 10)$
α_{SEAMAP}	Inverse of the stock availability coefficient inferred from SEAMAP index (A_{SEAMAP}), 1990–2008	$U(0.01, 10)$
ϕ_{NEFSC}	Inverse of the NEFSC survey's global efficiency (Φ_{NEFSC}), 1972–2008	$U(0.01, 1000)$
ϕ_{SEAMAP}	Inverse of the SEAMAP survey's global efficiency (Φ_{SEAMAP}), 1990–2008	$U(0.01, 1000)$
\hat{b}_{1972}	The 1972 expected depletion	$U(0.1, 10)$

¹ The 25th and 75th percentiles of this prior in arithmetic scale were 0.413 and 0.512, respectively.

² Prior for a parameter specific to M2.

³ When the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch were included.

Model configurations

Models M1 and M2 consisted of the base-case scenarios when using the prior PDF developed for the parameters r or r_0 and excluding the SESTF bycatch. Sensitivity to M1 and M2 outcomes was performed by using an alternative prior for r or r_0 , $U(0.01, 1.5)$, and including the SESTF bycatch (also treated as “known”) among fishery removals. The prior r or $r_0 \sim U(0.01, 1.5)$ has been tested on Whitemouth Croaker (*Micropogonias furnieri*) exploited in southern Brazil (Vasconcellos and Haimovici, 2006) and spans the range of possible r values for marine fish populations (Jensen et al., 2012). Models M1 and M2 configured with r or $r_0 \sim U(0.01, 1.5)$ were denoted as M1rU and M2rU, respectively; those models involving the SESTF bycatch were termed M1B and M2B.

A reviewer recommended that a diffuse normal prior centered on 0 for the MWET coefficient (α) would be appropriate. Consequently, an alternative prior $\alpha \sim N(0, 0.02)$ was used to examine its effects on inferences and especially on the statistics of model comparison. These models were denoted M2N, M2rUN,

and M2BN. For these models, estimates of α were constrained to be greater than -5 and the precision of 0.02 was so chosen to reflect moderate ignorance as advised by Kéry (2010) and Kéry and Schaub (2012).

Model goodness of fit and comparisons of models

The standardized median residuals by year for biomass or depletion ($stdr_t$) and for biomass indices ($std\omega_{ijt}$) were calculated as

$$stdr_t = \left[\log(B_t) - \log(\hat{B}_t) \right] / sd \Leftrightarrow$$

$$stdr_t = \left[\log(b_t) - \log(\hat{b}_t) \right] / sd,$$

where sd = the standard deviation of residuals in log-space for biomass or depletion; and

$$std\omega_{ijt} = \omega_{ijt} \tau_{ij} \text{ with } \omega_{ijt} = \log(i_{jt}) - \log(\hat{i}_{jt}).$$

Their time trajectories were monitored to check whether the stock biomass or depletion and the biomass indices conformed to the assumed lognormal distributions. Upon visual inspections of their scatter points, normal linear regressions were used to fit their trends.

The Bayesian approach to fitting the linear regressions and assessing their adequacy for the temporal trends in standardized residuals was adapted after Kéry (2010). The adequacy in question was based on the posterior predictive checks as reflected in Bayesian P -values and plots of the sum-of-squares for trends in replicated (“perfect”) standardized residuals against the sum-of-squares for trends in actual standardized residuals. When a model is adequate for the actual data, about half of the points lie above a 1:1 line on the plot. Equivalently, the Bayesian P -value is “close” to 0.5, and values “near” zero or one indicate doubtful fit of the model. Unfortunately, the range of Bayesian P -values for a good fit is unclear (Kéry and Schaub, 2012). By analogy to Ono et al.’s (2012) similar statistic, a Bayesian P -value of 0.45–0.55 was assumed close to 0.5.

The types of association between various standardized residuals and year were identified on the basis of 1) the signs of the posterior means and medians of the trend slopes, 2) the location of zero in the posterior distributions of slopes (i.e., whether the 95% BCI of these slopes covered zero), and 3) the computation of the probability of decline, P^* . This probability should be “close” to 0.5 (i.e., zero centered at the 95% BCI) for the lack of trend; its larger value (typically approaching one) indicated a negative trend and vice-versa for a smaller value approaching zero. The previous 3 procedures were jointly used to draw pragmatic conclusions because it was unclear what value of P^* indicated that a trend was not strong enough to be considered positive or negative.

The deviance information criterion (DIC) and the Bayes factor (BF) were used to compare various BSSB-DMs. Although DIC can be problematic in MCMC simulations, it is the most popular method of a Bayesian model fit and selection that is routinely implemented in the WinBUGS software. Typically, DIC selects among models by trading off goodness of fit and model complexity (Spiegelhalter et al., 2002; Wilberg and Bence, 2008) when competing models are fitted to the same data sets. It is given by

$$\begin{aligned} DIC &= 2\bar{D} - \hat{D} = \bar{D} + p_D, \\ D(\Theta) &= -2\log L(\Theta) - 2\log[P(O|\Theta)], \\ p_D &= \bar{D} - \hat{D}, \end{aligned} \quad (6)$$

where D = deviance (measure of goodness of fit);
 \bar{D} = the posterior mean deviance;
 \hat{D} = the deviance of posterior means of the elements in Θ ; and
 p_D = the “effective number of parameters.”

The statistic p_D is unstable to estimate, is not an integer, does not necessarily correspond with the number of parameters and, although it should be positive, can even be negative. The latter problem usually arises separately or jointly from ill-specifying priors or an ill-fitting model (data-prior conflict), and is symptomatic

of suspicious inferences or of non-normal posteriors of the parameters on which priors have been placed (Spiegelhalter et al., 2002).

The model with the smaller DIC is better supported by the data. In practice, comparisons of models are performed by using the difference in DIC (Δ DIC) among the competing models. As a rule of thumb, Δ DIC > 10 indicates models with no support for the model with the higher DIC; if $3 < \Delta$ DIC < 7, the model with the higher DIC has considerably less support; and Δ DIC < 2 indicates lack of substantial differences between models compared. All models with Δ DIC < 2 units from the lowest DIC model should receive consideration in making inferences (Spiegelhalter et al., 2002).

The BF comparing how well any two models M_x (associated with the null hypothesis) and M_y (corresponding to the alternative hypothesis) fitted the biomass indices was

$$BF_{yx} = \frac{P(O|M_y)}{P(O|M_x)}, \quad (7a)$$

where $P(O|M)$ = the marginal likelihood for $M \in \{M_x, M_y\}$ and was approximated as (Newton and Raftery, 1994; Kass and Raftery, 1995):

$$\hat{P}(O|M) = \left[\frac{1}{S} \sum_{s=1}^S P(O|\Theta_s) \right]^{-1}, \quad (7b)$$

where S = the number of simulations and

$$P(O|\Theta_s) = e^{-0.5D(\Theta_s)}.$$

The model that predicted the biomass indices better was considered to have more evidence supporting them and, hence, was preferred. Model preference relied on the guidelines of Kass and Raftery (1995) inferred from the natural log of BF (LBF), $LBF_{yx} = 2\log(BF_{yx})$. Here, $BF_{yx} < 1 \Leftrightarrow LBF_{yx} < 0$ supported M_x ; evidence for M_x was considered negligible if $1 < BF_{yx} < 3 \Leftrightarrow 0 < LBF_{yx} < 2$; and $BF_{yx} \geq 3 \Leftrightarrow LBF_{yx} \geq 2$ supported M_y .

The competing models included the same types of fishery removals. However, they differed in whether they included MWET, in the type of priors used, or in whether they included the SESTF bycatch.

Environmental anomalies

Assessing MWET effects on the Atlantic Croaker population off the U.S. east coast relied upon 3 approaches. First, in Equation 4 for M1, M1rU, and M1B, any potential environmental effects were implicitly lumped in the posterior process errors of these models, ε_t ($\varepsilon_t = \log(B_t) - \log(\hat{B}_t) \Leftrightarrow \varepsilon_t = \log(b_t) - \log(\hat{b}_t)$). These errors were expected to be theoretically positively correlated with MWET because MWET is considered to be the dominant environmental factor affecting the population dynamics of the species. The relationship between the posterior process errors and MWET was checked by regressing the credible medians of ε_{t+1} , for year $t+1$,

against MWET recorded from December of year t to March of year $t+1$, given that 1) juvenile, first-overwintering Atlantic Croaker born in year t recruit during the spring–summer months of year $t+1$ (ASMFC¹) and 2) the winter water temperatures prevailing during late year t –early year $t+1$ determine the t year-class strength and influence recruitment and average biomass in year $t+1$ (Hare and Able, 2007; Hare et al., 2010).

Second, variability of productivity for the Atlantic Croaker stock in response to climate anomaly was examined by regressing the credible medians of surplus production, G_t ($G_t = B_{t+1} - B_t + \sum R_{ft}$), and instantaneous surplus production, ρ_t ($\rho_t = \log[(G_t + B_t)/B_t]$), against MWET, because G_t and, especially, ρ_t are sensitive to environmental change (Jacobson et al., 2001; Mueter and Megrey, 2006). Finally, a linear effect of MWET was considered statistically supported if zero was outside the 95% BCI of the coefficient controlling MWET impacts, consistent with runs of models M2N, M2rUN, and M2BN.

Visual inspections of the scatter points indicated that simple linear regressions were appropriate to fit the relationships between the process error, surplus production, or instantaneous surplus production and MWET. The fitting and adequacy of these regressions, the types of association between the regressed variables, and the linear effect of MWET were determined by the techniques outlined above (see also Grosbois et al., 2008; Wilson et al., 2011).

Stock status

The ratios H_t/\hat{H}_{MSY} ($H_t = \sum R_{ft}$) and B_t/\hat{B}_{MSY} were compared with the 1:1 ratio—herein considered a criterion of status determination—to judge whether overfishing was occurring ($H_t/\hat{H}_{MSY} > 1$) or whether the stock was overfished ($B_t/\hat{B}_{MSY} < 1$). The probability that $H_t/\hat{H}_{MSY} > 1$, $P(H_t/\hat{H}_{MSY} > 1)$, and the probability that $B_t/\hat{B}_{MSY} < 1$, $P(B_t/\hat{B}_{MSY} < 1)$, were used to estimate the risks of overfishing and of overfished status, respectively (Jiao et al., 2009). $P(H_t/\hat{H}_{MSY} > 1)$ and $P(B_t/\hat{B}_{MSY} < 1)$ corresponded with the proportions of iterations where the most credible means of $H_t/\hat{H}_{MSY} > 1$ and the most credible means of $B_t/\hat{B}_{MSY} < 1$. The previous risk of overfishing relate to M1, M1rU, and M1B. The risk of overfishing for M2 and its variants was $P(H_t/\hat{H}_{MSY_t} > 1)$. These control rules do not conform to the legal sense used by the NMFS, but they are consistent with the rules considered in the ASMFC¹ BDMs.

Results

Goodness of fit and comparisons of models

The standardized median residuals for stock biomass and biomass indices were comparable and trended similarly across models (Fig. 2). Their credible estimates

ranged from -1.8 to 1.2 , except for the disproportionate (-5.2 to -4.2) 1972 residuals for the NEFSC index, which indicated excessive overestimation of the corresponding observed values (Fig. 2, C and D). The latter residuals were clearly outliers and were omitted in the residual diagnostics.

The plots of discrepancy checks (not shown) and the Bayesian P -values (0.52–0.55) indicated that the fitted linear regressions were adequate for the trends in various standardized residuals. The negative posterior means and medians of all trend slopes evidenced consistent, negative trends in the residuals. Regardless, at a 0.95 probability, those trends stabilized at zero (i.e., the 95% BCIs of their slopes included zero). Moreover, the probabilities of decline were closer to 0.5 than to one ($P^*=0.58$ – 0.74 for biomass, $P^*=0.52$ – 0.68 for NEFSC index, and $P^*=0.62$ – 0.64 for SEAMAP index; the largest P^* -values were associated with residuals from M1rU and M2rU), and, indeed, the posterior distributions of those slopes were bell-shaped and centered near zero. This result agreed with fair fits of biomass indices that were nearly identical across models (Fig. 3) and indicated that the lognormal distribution was a reasonable assumption for the latent biomass and observed indices.

The means of most parameters were slightly different from the medians owing to right-(or left-) skewed posterior marginal distributions (to conserve space, the related details were not provided but are available upon request). Such distributions were therefore slightly better summarized by the percentiles. For competing models with or without MWET, the posterior means and percentiles of the parameters were of the same magnitude. In comparison with base M1 and M2, M1 and M2 sensitivity runs showed the following aspects about the stock productivity, management benchmarks, and initial depletion. Use of the prior r or $r_0 \sim U(0.01, 1.5)$ led to 1) nearly doubling the rate of population increase (note: median r =median $r_0 \approx 0.47$ for base M1 and M2, respectively), \hat{H}_{MSY} , and \overline{MSY} ; 2) predicting similar posterior medians for B_∞ ($\approx 220,000$ t) and \hat{B}_{MSY} ; and 3) estimating lower (75–78%) posterior medians of the 1972 depletion, \hat{b}_{1972} (note: $\hat{b}_{1972} = 0.07$ for base M1 and M2).

Inclusion of the SESTF bycatch yielded comparable posterior medians for r , r_0 , or \hat{H}_{MSY} but increased the credible estimates of B_∞ and \overline{MSY} by about 1.27 times and doubled the 1972 depletion (b_{1972}). As a result, for M2 variants in particular, year-specific posterior medians of the parameters r and \hat{H}_{MSY} estimated by using M2rU were nearly twice the medians produced by M2 and M2B (Fig. 4); year-specific \overline{MSY} from M2B were on average 1.3 times higher than those estimates from M2 but averaged 81% of those estimates from M2rU. It was also observed that, in all models with MWET, the r (and related metric) time series mimicked the MWET trend well, but those time series where the prior $G(0.01, 0.001)$ was used for the MWET coefficient α varied less than those time series estimated with the

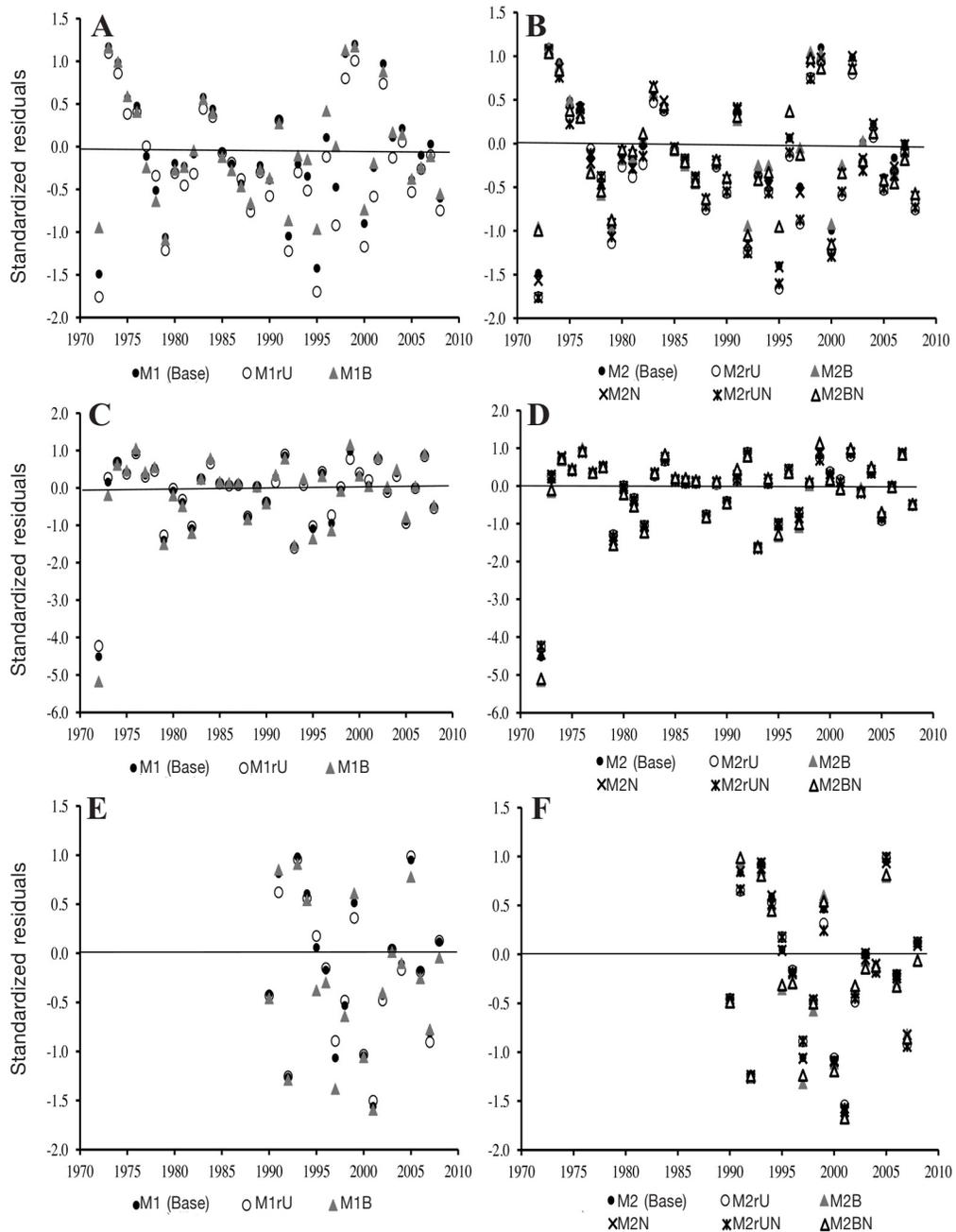
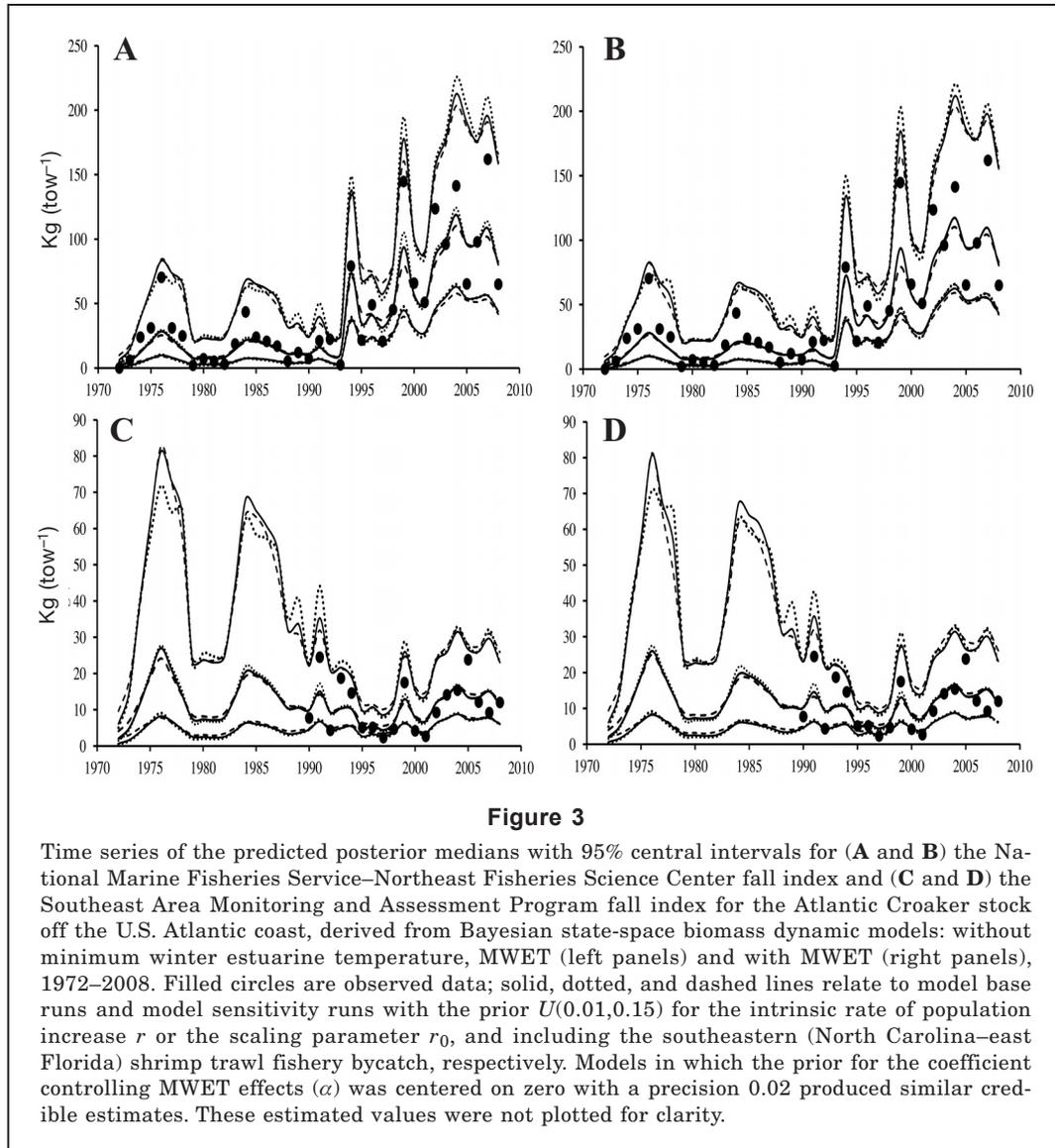


Figure 2

Time series of standardized median residuals for (A and B) biomass, 1972–2008; (C and D) the National Marine Fisheries Service–Northeast Fisheries Science Center fall index, 1972–2008; and (E and F) the Southeast Area Monitoring and Assessment Program fall index, 1990–2008 derived for the Atlantic Croaker stock off the U.S. Atlantic coast by using Bayesian state-space biomass dynamic models: without minimum winter estuarine temperature, MWET (model 1, M1; left panels), and with MWET (model 2, M2; right panels). Residuals relate to model base runs, M1 (Base) and M2 (Base), and to their sensitivity runs: in other words, M1 and M2 using the prior $U(0.01, 0.15)$ for the intrinsic rate of population increase r or the scaling parameter r_0 , M1rU and M2rU; and M1 and M2 including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch, M1B and M2B. M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which the prior for the coefficient controlling MWET effects was centered on zero with a precision of 0.02.



prior $\alpha \sim N(0,0.02)$ (Fig. 4). The stock availability coefficient associated with the NEFSC index (hence, the NEFSC Bottom Trawl Survey catchability) was 8 times higher during 1994–2008 ($A_{\text{NEFSC94-08}} = 0.7\text{--}0.8$) than during 1972–93 ($A_{\text{NEFSC72-93}} \approx 0.11$). The stock availability coefficient, global efficiency ($\approx 1.11 \times 10^{-3}$), and catchability by survey and period were insensitive to model configurations.

The components of the DIC statistics (Table 2) for models without MWET were the NEFSC index, SEAMAP index, depletion time series, and process error variance. They included the coefficient α for models incorporating MWET. Model fits were largely dominated by biomass indices (98–99% of DIC statistics, of which the NEFSC index amounted to 68–73%). The total estimates of p_D were positive and consistent across models, supporting the evidence

that all models generally had the same number of parameters.

Other DIC statistics for models of the study were greater for (base and sensitivity) M2 than for (base and sensitivity) M1 and, among model configurations, were the least for M1rU and M2rU. The former result for competing models, with or without MWET, was mainly due to the extra parameter α that clearly had no explanatory power. The DIC associated with α was 4.17 for all M2s and represented 92–101% of ΔDIC (Table 2). For the competing models with alternative priors for the parameter r or r_0 , lower DIC statistics for M1rU and M2rU resulted from the decrease in \bar{D} and \hat{D} for biomass indices—a decrease that largely contributed to ΔDIC . This finding indicates an improvement in fit as also evidenced by a slight increase in the corresponding p_D . However, this situation was counterbalanced by

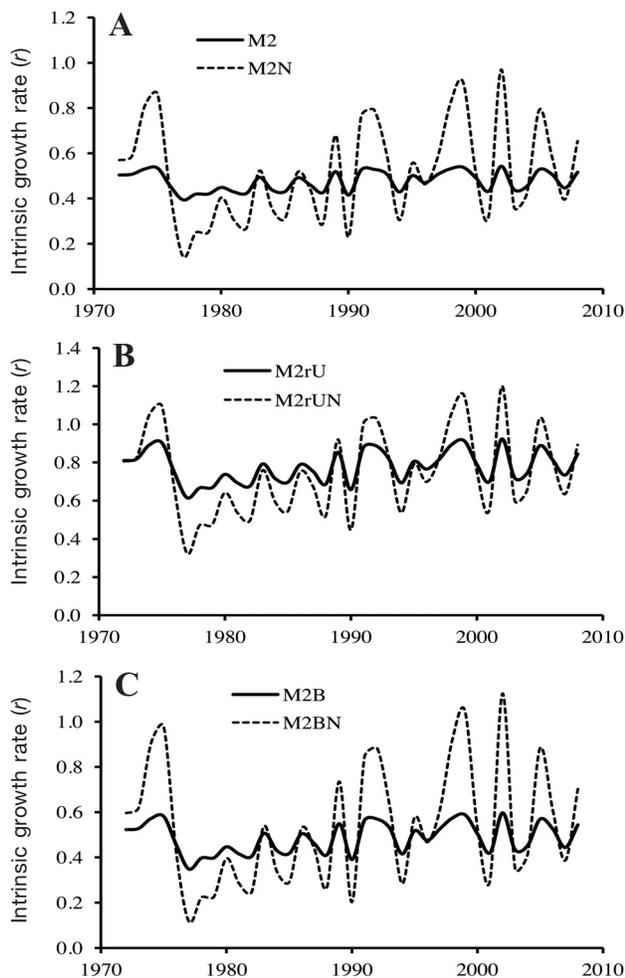


Figure 4

Time series of the predicted posterior medians of the intrinsic rate of population increase (r) for the Atlantic Croaker stock off the U.S. Atlantic coast derived from Bayesian state-space biomass dynamic models incorporating the minimum winter estuarine temperature (M2), 1972–2008. Results relate to (A) M2 base runs, (B) M2 sensitivity runs with the prior $U(0.01, 0.15)$ for the scaling parameter r_0 (M2rU), and (C) M2 sensitivity runs with the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch (M2B). M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which the prior for the coefficient controlling MWET effects (α) was centered on zero with a precision of 0.02. The 95% central intervals of r were not plotted for clarity.

an increase in \bar{D} and \hat{D} associated with the depletion component, with $\hat{D} > \bar{D}$ leading to negative p_D values. This result was symptomatic of an ill-specified (inappropriate?) prior, ill-fitted models, or was symptomatic of both and, hence, of unreliable inferences from M1rU and M2rU runs, although the corresponding overall p_D estimates were positive.

The DIC statistics for M2N, M2rUN, and M2BN did

not include negative p_D estimates. On the basis of Δ DIC, they were comparable with those DIC statistics for their counterparts without MWET and, therefore, should be considered for making inferences (Table 2). In short, except M2N, M2rUN, and M2BN, $|\Delta$ DIC $\in [4.13, 5.70]$: models with greater DIC were substantially less well supported despite among-model similarity of residual patterns and magnitude (Fig. 2). (Should the actual deviance for the parameter α be dropped from the DIC for M2, M2rU, and M2B, then $|\Delta$ DIC $\ll 2$. This result would indicate lack of differences between models with and without MWET (M1, M1rU, and M1B), and both types of models should be considered for making inferences. However, because α would still have no explanatory power [i.e., the DIC for M2, M2rU, and M2B would still be slightly larger than the DIC for M1, M1rU, and M1B], the parsimonious models [without MWET] would still be preferred). On the other hand, the LBF statistic consistently rejected models with the prior r or $r_0 \sim U(0.01, 1.5)$, models incorporating MWET, or both models; even upon some evidence against models without MWET, this evidence was weak (Table 2).

Therefore, comparisons of models indicated that the complexity of (base and sensitivity) M2 brought about by the introduction of MWET was not warranted by the data. Furthermore, the models with the prior r or $r_0 \sim U(0.01, 1.5)$ were discredited on the grounds that the values for their depletion component were negative and because of the disagreement between DIC and LBF statistics. Preference was given to results from the LBF statistic for 2 reasons. The BF is among the formal solutions to the model-choice problem (Plummer, 2008). Although Equation 7b is computationally unstable, it is consistent as the simulation size S increases and, in practice, often gives results that are accurate enough for interpretation on the logarithmic scale (Kass and Raftery, 1995). The whole process of model comparisons with DIC and BF (LBF) statistics therefore selected M1 and M1B only. Unless otherwise indicated, the following results related to M1 and M1B.

Extent of climate forcing

The plots of discrepancy checks (not shown) and the Bayesian P -values (0.53–0.55) indicated that the fitted linear models were adequate for the relationships between 1) the process errors and MWET, 2) surplus production and MWET, and 3) instantaneous surplus production and MWET (Fig. 5). These relationships were positive because positive values had most of the mass under the posterior, bell-shaped distributions of their slopes. This result was reflected in positive credible means and medians of those slopes and by large posterior probabilities of increase ($P^* > 0.88$).

Table 2

Results of a comparison of Bayesian state-space biomass dynamic models based on the deviance information criterion (DIC) and Bayes factor (BF) or log Bayes factor (LBF): without minimum winter estuarine temperature, MWET (base model 1, M1), and with MWET (base model 2, M2) for the Atlantic Croaker population off the U.S. Atlantic coast, 1972–2008. Sensitivities to M1 involving the prior $U(0,01,1.5)$ for the intrinsic rate of population increase r and inclusion of the southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) bycatch led to models M1rU and M1B, respectively. Sensitivities to M2 involving the prior $U(0,01,1.5)$ for the scaling parameter r_0 and inclusion of the SESTF bycatch led to models M2rU and M2B. M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which a diffuse normal prior centered on zero, with a precision of 0.02, was used as sensitivity to the prior for the coefficient controlling the effect of MWET α . \bar{D} and \hat{D} are mean model deviance and model deviance at the parameter mean, respectively; p_D is the effective number of parameters; Δ DIC is the difference in DIC among competing models. The models compared by using BF and LBF are the same as those models compared by using Δ DIC.

Model	Component ¹	\bar{D}	\hat{D}	p_D	DIC	Δ DIC	BF	LBF
M1	NEFSC	318.42	308.59	9.84	328.26			
	b_t	0.71	0.51	0.20	0.90			
	SEAMAP	114.79	110.40	4.39	119.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	438.95	424.53	14.42	453.37			
M1rU	NEFSC	314.14	304.02	10.12	324.26			
	b_t	1.19	1.28	-0.08	1.11			
	SEAMAP	113.01	108.53	4.48	117.49			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	433.38	418.87	14.52	447.90	M1 vs. M1rU: -5.47	1.02	0.05
M1B	NEFSC	330.48	321.10	9.38	339.86			
	b_t	0.31	0.10	0.21	0.51			
	SEAMAP	117.26	113.65	3.61	120.87			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	453.07	439.88	13.20	466.27			
M2	NEFSC	318.30	308.54	9.76	328.06			
	b_t	0.71	0.46	0.25	0.96			
	SEAMAP	115.17	110.83	4.34	119.51			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	443.39	429.05	14.34	457.73	M1 vs. M2: 4.36	1.28	0.49
M2rU	NEFSC	313.66	303.57	10.10	323.76			
	b_t	1.20	1.22	-0.02	1.19			
	SEAMAP	113.49	109.10	4.39	117.88			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	437.56	423.10	14.47	452.03	M1rU vs. M2rU: 4.13 M2 vs. M2rU: -5.70	0.05 0.04	-6.15 -6.59

The process errors from M1 and M1B increased with MWET at a 0.95 probability given that zero was outside the 95% BCIs of the mean slopes (0.133 and 0.124) of the corresponding relationships: those 95% BCIs were (0.017, 0.247) and (0.035, 0.212), respectively. Here, $P^* > 0.98$. On average, these relationships explained 14% and 19.5% of the variation in the process errors. In contrast, the 95% BCIs of the slopes for the relationships between surplus production or instantaneous surplus production and MWET included zero. The increase in these productivity metrics with MWET was therefore negligible at a 0.95 probability.

Estimates from M2N, M2rUN, and M2BN of the posterior credible medians of the coefficient for MWET

(α) were 0.42, 0.29, and 0.50, respectively, suggesting positive effects of MWET on the Atlantic Croaker production dynamics. However, the related 95% BCIs equaled (-0.57, 1.25), (-0.48, 1.22), and (-0.32, 1.19): these effects were negligible at a 0.95 probability. This result was consistent with that associated with the BF statistic.

Model trends

The biomass ratios, B_t/\hat{B}_{MSY} (Fig. 6, A and B), trended like the depletions (B_t/B_{∞} ; not shown), which themselves tracked the variations of the NEFSC index well. They were characterized by low precision before 1990,

Table 2 (continued)

Model	Component ¹	\bar{D}	\hat{D}	p_D	DIC	Δ DIC	BF	LBF
M2B	NEFSC	330.08	320.71	9.37	339.46			
	b_t	0.28	0.07	0.22	0.50			
	SEAMAP	117.95	114.63	3.68	121.63			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	457.52	444.25	13.27	470.80	M1B vs. M2B: 4.52	0.10	-4.51
M2N	NEFSC	317.22	307.33	9.89	327.11			
	b_t	0.82	0.51	0.31	1.13			
	SEAMAP	115.64	111.40	4.23	119.87			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	439.26	424.83	14.43	453.69	M1 vs. M2N: 0.32	2.32	1.69
M2rUN	NEFSC	313.96	303.66	10.26	324.22			
	b_t	1.27	1.16	0.11	1.38			
	SEAMAP	113.97	109.69	4.28	118.24			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.037	5.037	0.00	5.037			
	Total	434.77	420.12	14.65	449.42	M1rU vs. M2rUN: 1.53	1.76	1.13
M2BN	NEFSC	328.73	319.19	9.54	338.28			
	b_t	0.36	0.09	0.27	0.63			
	SEAMAP	118.23	114.49	3.74	121.98			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	452.91	439.36	13.56	466.47	M1B vs. M2BN: 0.20	2.06	1.45

¹ The components accounted for in DIC calculations for models without MWET were the Northeast Fisheries Science Center (NEFSC) fall index, the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index, the depletion time series b_t , and the process error variance σ_p^2 ; the components for models incorporating MWET also included the coefficient α . Note that the DIC calculations should only include the components for indices and the depletion, but WinBUGS unexpectedly included the process error variance and α as well.

especially when the commercial removals, the SESTF bycatch, or both suddenly increased. (Following low biomasses in the early 1970s and 1980s, the models predicted large but imprecise depletion levels that were needed to support the upsurge of the fisheries removals). The biomass ratios indicate an overfished stock of Atlantic Croaker in most years except in the mid-1970s, mid-1980s, and perhaps in 1991, 2004, and 2007 when the NEFSC index had peaked after years of low total fishery removals.

The harvest ratios, H_t/\hat{H}_{MSY} (Fig. 6, C and D), showed trends opposite of the biomass ratios, and their precision was generally consistent over time. They indicated that the Atlantic Croaker stock likely experienced overfishing during 1993–2001.

The risks for the Atlantic Croaker stock being overfished (Fig. 6, E and F) coincided with the lowest estimates for the NEFSC index and culminated in years when both this index was lowest and the estimates of total fishery removals in the preceding years were highest (e.g., 1972–74, 1978–83, and 1995–2001). This result reflected the model structures and behaviors in that, in a given year, the estimated stock biomass was

largely driven by that year's NEFSC index and the total fishery removals of the preceding year. On the other hand, the models interpreted the magnitude of total fishery removals as a signal of overfishing risk: this one was highest in years of larger total fishery removals (1993–2001), lowest otherwise (Fig. 6, E and F). For the period of 2002–08, the risk of overfishing averaged 0.2 and the risk of the overfished status averaged 0.7.

Biomass depletions, ratios, and overfished risks were insensitive to model variants, including the rejected ones, because all models fitted the biomass indices equally. The harvest ratios and risks of overfishing trended similarly across models. In some years, however, the latter statistic was largest for models including the SESTF bycatch.

Discussion

We used BDMs to improve understanding of the climate effects on Atlantic Croaker production dynamics along the U.S. Atlantic coast. An age-structured production model has been applied to address the same

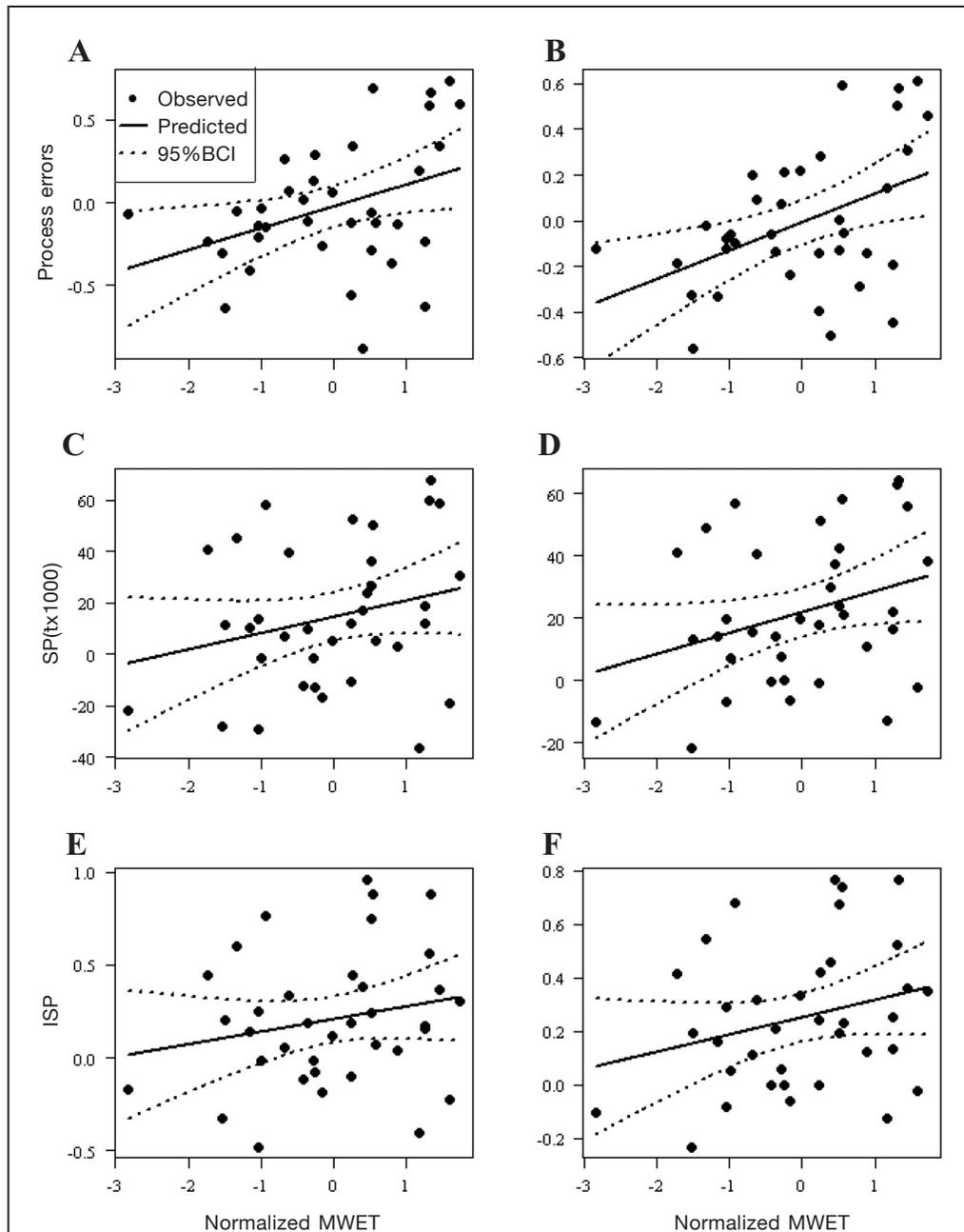
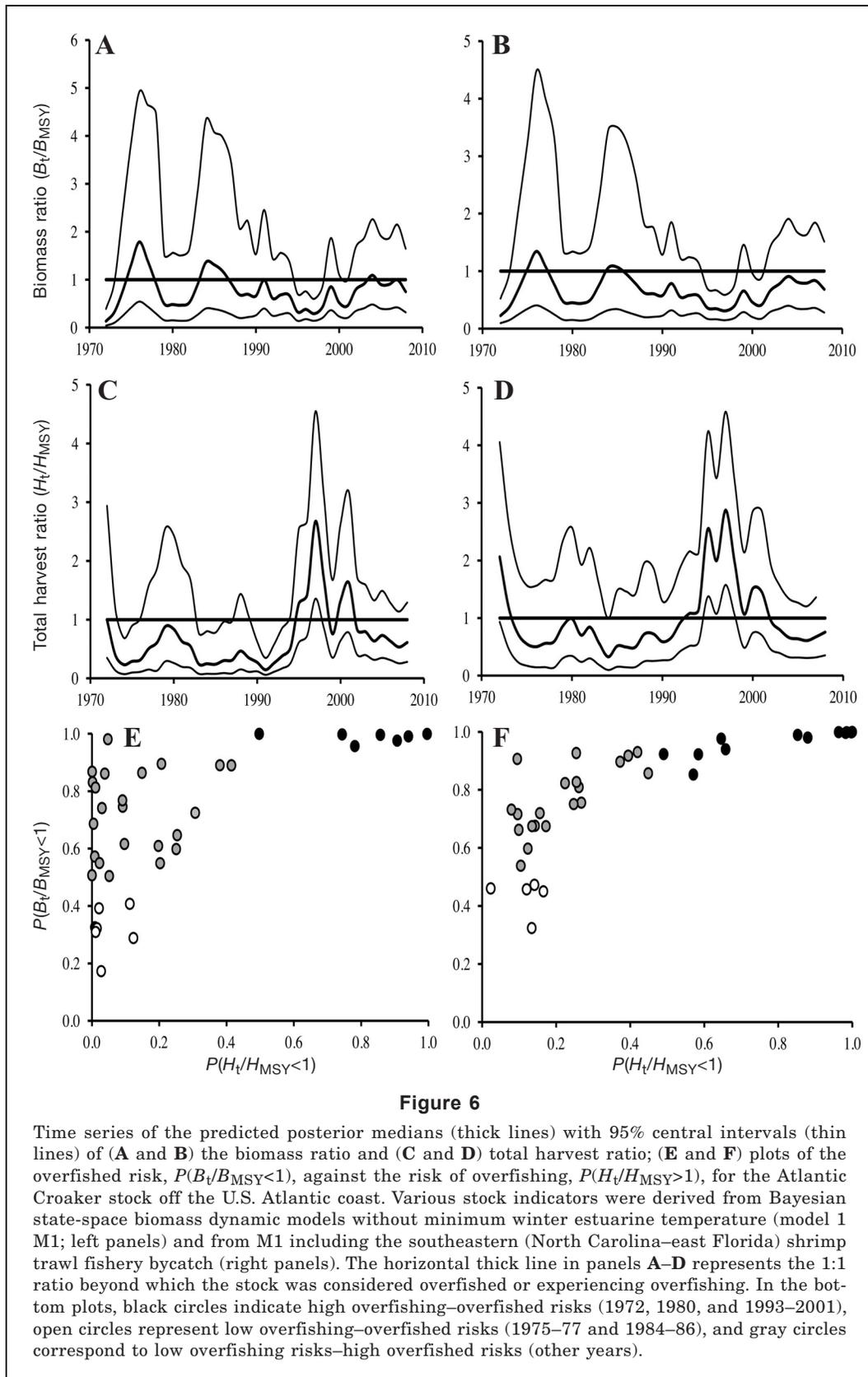


Figure 5

Relationships between the posterior medians of (A and B) process errors, (C and D) surplus production (SP), and (E and F) instantaneous surplus production (ISP) and the normalized minimum winter estuarine temperature, MWET. The process errors, SP, and ISP were generated from the Bayesian state-space biomass dynamic model without MWET (model 1, M1; left panels) and from M1 including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch (right panels) for the Atlantic Croaker stock off the U.S. Atlantic coast, 1972–2008. They were treated as observed data. Their fitting with simple linear regressions generated the predicted process errors, SP, and ISP. The insert in panel A shows the legend, including for the 95% Bayesian central intervals (95%BCI), common to all plots.



issue (Hare et al., 2010). However, diversifying investigation models was in part consistent with ASMFC's assessment needs and Hare et al.'s (2010) suggestion for this fishery resource when faced with changes in anthropogenic activity (here, fishing), environmental forcing, and also with parameter uncertainty. BDMs are typically suitable when fishery data are limited to aggregate catch and effort or indices of stock biomass (Hilborn and Walters, 1992; Prager, 1994). Regardless, even in "data-rich" jurisdictions, various stock-assessment teams customarily implement them to support the results of the more sophisticated, data-hungry models. Jacobson et al. (2002) and MacCall (2002) recommended their systematic use as supplemental assessment tools because, in spite of their simplicity and alleged lack of realism, they can be the basis of useful management actions (Ludwig and Walters, 1985; Laloë, 1995).

Investigations have focused on the alleged winter-temperature effects on Atlantic Croaker productivity that occur during the prerecruit stages of the species (Joseph, 1972; Norcross and Austin²; Lankford and Targett, 2001a, 2001b; Hare and Able, 2007; Hare et al., 2010). Age- and stage-structured fisheries models are used to investigate environmental effects on population changes through the deviations from an "average" or "virgin" recruitment or through stock-recruitment models, where environmental covariates, along with unexplained random errors, are assumed to influence the recruitment processes and variability (e.g., Iles and Beverton, 1998; Levi et al., 2003; Maunder and Watters, 2003; Hare et al., 2010). These effects can be incorporated into density-dependent, density-independent, or both types of parameters of stock-recruitment models.

By analogy to stock-recruitment models, MWET was introduced into the parameter r that, in surplus-production models, is the counterpart of the density-independent parameter of stock-recruitment models, and process errors characterized all model parameters. Preference was given to the Bayesian state-space modeling framework because of its anticipated flexibility in addressing simultaneously various types of errors and parameter uncertainty and because it was deemed suitable for shedding light on the ability of BDMs to detect MWET effects. A corollary of these investigations was the examination of the extent of such effects on the Atlantic Croaker stock status.

Focusing MWET effects on r was, in conjunction with available fishery data (i.e., fisheries removals and survey indices only), the simplest scenario of implemented BDMs. However, this procedure was also dictated by the need of parsimony in statistical analysis, thereby favoring simple models. If there were supporting data and evidence on changes in habitat conditions—usually affecting B_{∞} , in other words, the density-dependent parameter (e.g., Jacobson et al., 2005)—or in fisheries effective effort and catchability, it may have also been convenient to consider their effects and interactions on Atlantic Croaker productivity. Information about these

factors ultimately needs to be gathered and equally accounted for in future analyses.

The analysis led to mixed outcomes. On the one hand, the positive and significant correlations between the process errors from M1 or M1B and MWET supported the hypothesis that MWET may be playing a role in biomass variability of Atlantic Croaker on the U.S. Atlantic coast. Increased growth or increased recruitment during years of warmer winters would therefore enhance biomass production in subsequent years. However, such relationships were weak in that only 14% and 19.5% of process errors were related to the variation in MWET. On the other hand, there were possible positive relationships between surplus production or instantaneous surplus production and MWET, but the relationships were statistically insignificant. The lack of a relationship between surplus production and an environmental covariate, however, is not unusual.

In contrast, it was surprising that instantaneous surplus production vs. MWET and surplus production vs. MWET exhibited similar and insignificant relationships. Instantaneous surplus production is usually more sensitive to environmental change than is the corresponding surplus production (Jacobson et al., 2001). Likewise, the hypothesis of MWET effects on the Atlantic Croaker production dynamics had no support of the 95% BCIs for the coefficient controlling MWET effects (α) upon specifying its prior as $\alpha \sim N(0, 0.02)$. Weakness and absence of the aforementioned relationships corroborated the fact that BSSBDMs incorporating MWET (although conceptually interesting and ecologically plausible) did not statistically outperform those BSSBDMs without MWET nor did it predict significantly different metrics of stock status. In comparison with Hare et al.'s (2010) results, this study revealed that correlations between MWET and a metric of Atlantic Croaker productivity can appear and disappear or be weak with a modeling approach.

Surplus production models with environmental effects have sometimes improved understanding and description of the performance of fished populations and ecosystems when all key control variables and causal mechanisms have been unambiguously identified, understood, and accounted for (e.g., Fréon, 1988; Evans et al., 1997; Yáñez et al., 2001; Jacobson et al., 2005; Mueter and Megrey, 2006; Thiaw et al., 2009; some contributions in Bundy et al., 2012). Exceptions to such favorable situations exist (Laloë, 1988; Fogarty et al., 2012; this study). Here, BDMs failed to detect MWET effects adequately because of 4 possible major reasons. First, in the process errors–MWET relationships, the remaining, unexplained 81–86% of the variation in the process errors may be rooted in other, yet unknown environmental anomalies. This outcome indicated the possibility that MWET (inter)acted with other ecological factors (e.g., change in other habitat conditions).

Second, random errors and a well-established underlying environmental anomaly may not be linked linearly or may even be unrelated because environmental

fluctuations are not necessarily random (Jensen, 2002; Sinclair and Crawford, 2005). Environmental variations may themselves be driven by other, direct or indirect anthropogenic or natural events, as would have happened for MWET (e.g., Connelly et al.⁷; Fogarty et al.⁸). Third, elusive relationships may have been due to the shortness of the time series for the regressed variables.

Finally, surplus-production models are oversimplifications of the population dynamics in the form of just 2 or 3 parameters (Laloë, 1995; Keyl and Wolff, 2008). Other possible reasons for the blurring or weakening of the impacts of MWET on Atlantic Croaker productivity could be the noisy nature of the tuning indices especially since 1990, the lack of fishing effort that precluded the partitioning of any roles between fishing intensities and MWET, and the functional relationship between the parameter r and MWET. In reality, this function is unknown, and alternative functional forms (e.g., Fréon, 1988; Stenseth et al., 2002; Rose, 2004; Hatton et al., 2006) are conceivable and deserve testing as well.

Overall, the trends generated by this study behaved like those trends obtained through runs of nonequilibrium production models with A Stock Production Model Incorporating Covariates (ASPIC, vers. 5.34. 9, which is included in the NOAA Fisheries Toolbox, <http://nft.nefsc.noaa.gov/ASPIC.html>) software and Excel spreadsheets (ASMFC¹). Various implementations of BDMs also produced similar estimates of the initial depletion, MSY , and B_{MSY} , and conveyed a common message that the Atlantic Croaker stock was exposed to a relatively low risk of overfishing in the 2000s. But this analysis showed differences from ASMFC's¹ implementations about the opposing stock status prior to the 2000s (Fig. 6). Contrary to ASMFC's¹ results, this study indicates frequent episodes of overfishing, often with high risks of being overfished, that marked the Atlantic Croaker stock during the period of records. Likewise, overfishing of the Atlantic croaker stock may have been high during 1993–2001 (along with high risks for this stock being overfished) but were low in most years before 1993.

The causes underlying these discrepancies would require dedicated experimental designs for BDM per-

formance analyses, which were not the focus of this study. However, all other things being equal (i.e., no errors pertaining to fishery removals and parameter estimation), the conflicts in the performance of, for example, ASPIC and the BDMs used in this study, can be attributed to model uncertainty (Caddy and Mahon, 1995; Harwood and Stokes, 2003), itself inherently embedded in the general scientific uncertainty (Ralston et al., 2011; Rothschild and Jiao, 2011).

These conflicts may have been jointly or separately rooted in at least 3 major factors. The first factor was the difference in BDM structures (continuous formulation for ASPIC vs. discrete formulation in this study) and the way the corresponding estimation approaches (frequentist vs. Bayesian) dealt with uncertainty. The second factor related to the BDM behaviors resulting from the constrained starting values (ASPIC), nonuse of starting values (this study), and differing estimable parameters. The third and, perhaps, most important (Polacheck et al., 1993; Ono et al., 2012) factor was the error structures assumed including the specifications of the priors' PDFs (observation error for ASPIC vs. observation and process errors in this study). Note that observation errors are year-specific, whereas process errors can propagate over time (Kimura et al., 1996).

This study generated inconclusive, somewhat conflicting results about MWET effects on the production dynamics of Atlantic Croaker. Specifically, these effects were associated with a coefficient without explanatory power or with various linear relationships that proved weak or negligible in justifying addition of a related parameter in BDMs. If BDMs are to be used for assessing the Atlantic Croaker stock, it appears reasonable to continue performing them without considering MWET. Unambiguously discerning the extent of MWET effects through BDMs will perhaps be possible when longer time series of relevant fishery data, winter estuarine temperature (or, preferably, direct estimates of kills caused by cold winter), and other environmental factors will be gathered and accounted for together.

Conclusions

Given the well-established effects of the changes in winter water temperatures on the production dynamics of Atlantic Croaker along the U.S. Atlantic coast, the title of Keyl and Wolff's (2008) article deserves paraphrasing: what can (assessment) models do to track such effects, modify the perception of the stock, and better guide management? The present study has attempted to answer this question through state-space BDMs with and without MWET. BDMs incorporating MWET were not statistically supported by the data and did not outperform BDMs without MWET. The retained BDMs without MWET were associated with process errors, surplus production, and instantaneous surplus production that indicated that MWET had positive effects on Atlantic Croaker productivity. However,

⁷ Connelly, W., L. Kerr, E. Martino, A. Peer, R. Woodland, and D. Secor. 2007. Climate and saltwater sport fisheries: prognosis for change. Technical Report Series No. TS-537-07 of the University of Maryland Center for Environmental Science. Ref. No. [UMCES]CBL 07-119. Chesapeake Biological Laboratory, UMCES, Solomons, MD. [Available at: <http://www.seasonsand.org/pdfs/Saltwater%20Fisheries.pdf>; accessed May 2012.]

⁸ Fogarty, M., L. Incze, R. Wahle, D. Mountain, A. Robinson, A. Pershing, K. Hayhoe, A. Richards, and J. Manning. 2007. Potential climate change impacts on marine resources of the northeastern United States. Northeast Climate Impacts Assessments (NECIA). [Available at: http://www.northeast-climateimpacts.org/pdf/miti/fogarty_et_al.pdf; accessed May 2012.]

these effects were statistically significant but weak (i.e., explaining smaller amounts of the variation in the dependent variables) or insignificant, hence negligible. With the available data, BDMs failed to fully capture MWET effects on the Atlantic Croaker population, although these effects are notorious. Accumulation of longer time series of data on fisheries, surveys, winter water temperature, and other relevant covariates (e.g., indices of habitat conditions, winter-induced kills of juveniles), warrant further investigations on BDM performance and their ability to detect cold winter effects on the Atlantic Croaker population dynamics along the U.S. Atlantic coast.

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Appendix 1

Characteristics of the Bottom Trawl Surveys of the Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service, and of the multiagency Southeast Area Monitoring and Assessment Program (SEAMAP) Coastal

Surveys¹. Data obtained from these surveys were used to develop biomass indices for the population of Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Atlantic coast during the period of 1972–2008.

Attributes	NEFSC	SEAMAP
Start year	1963	1986
Area coverage	Cape Hatteras (North Carolina, NC)–Cape Cod (Massachusetts)	Cape Hatteras (NC)–Cape Canaveral (Florida)
Targets	Finfish and invertebrates	Finfish, elasmobranchs, sea turtles, invertebrates, and algae
Objectives	Monitor trends in abundance, distribution, and life history traits	Monitor trends in abundance and reproductive conditions
Covariates	Latitude, longitude, salinity, temperature, weather, and hydrographic parameters	Salinity, water and air temperatures, weather, and hydrographic parameters
Design	Stratified random (strata: depth ranges; inshore vs. offshore)	Stratified random (strata: depth contours; depth ranges ²)
Sampling gear	#36 Yankee otter trawl (5-fathom legs; 1,000-lb polyvalent door; 0.5-inch codend liner)	Trawl body: #15 twine and 47.6-mm stretched mesh codend; #30 twine and 41.3-mm stretched mesh codend
Tow duration	30 minutes	20 minutes (daylight hours)
Sampling intensity	Fall (inshore) surveys since 1963; spring surveys since 1968; intermittent summer and winter surveys	Surveys in spring (April–May), summer (July), and fall (October)
Evaluation	Fall surveys regularly encountered Atlantic Croaker since 1972; targeted multiple age classes (0–13 year-old fish)	Most zero tows in spring surveys; only fall surveys were consistent since 1990; targeted multiple age classes (0–6 year-old fish)

¹ Formerly known as Shallow Water Trawl Surveys; conducted by the South Carolina Department of Natural Resources, Marine Resources Division.

² Deeper strata (10–19 m) sampled during 1989–2000; abandoned in 2001 to concentrate on shallower depth zones.

Appendix 2

A prior probability distribution was developed for the intrinsic rate of population increase for Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Atlantic coast.

The basic demographics of Atlantic Croaker (Appendix 3) were combined in a Leslie matrix projection framework (McAllister et al., 2001) to construct a prior probability density function for the intrinsic rate of population increase, r (Table 1). The mean reproductive rate-at-age (R_a) was scaled by 10^{-5} to ensure that for all year (50)×replicate (2000) combinations, the resulting r values ranged from 0.01 to 1.5, as seems plausible for marine fish populations (Vasconcellos and Haimovici, 2006; Jensen et al., 2012):

$$R_a = 10^{-5} (p_a SR_a F_a). \quad (\text{A1})$$

where p_a , SR_a , and F_a are age-specific proportion of mature individuals, sex-ratio (assumed to be 0.5), and mean fecundity, respectively. Implicit in the scaling factor of 10^{-5} for R_a was the assumption that about 11.513 represented the cumulative mortality from egg fertilization to the recruiting age-group (here age-0) in the Leslie population model. Fecundity-at-age was estimated as

$$F_a = \beta \{L_\infty [1 - \exp(-K(\alpha - \alpha_0))]\}^\gamma, \quad (\text{A2})$$

where β and γ are parameters of the fecundity (number of eggs)–total length (mm) relationship; L_∞ , K , and α_0 are parameters of the von Bertalanffy growth function.

Lognormal distributions were assumed for both natural mortality and reproductive rate-at-age (i.e., they were log-transformed and treated as expected means).

Appendix 3

Demographic inputs for the construction of the prior probability distribution of the intrinsic rate of population increase for Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Atlantic coast. The von Bertalanffy growth

Monte Carlo samplings were performed with R software (vers. 2.15.3; R Development Core Team, 2013) with an age-independent coefficient of variation (CV) equal to 0.3 for both parameters (however, a CV=0.3 for the reproductive rate was insensitive to the natural mortality CV $\in [0.1, 1.0]$ in terms of r summary statistics and distributions). The CVs used were a single realization of all possible CV combinations for natural mortality and reproductive rate. They were preferred because, unlike the r estimates in many other trials, the corresponding r estimates fell within and spanned the 0.01–1.5 interval (note: reproductive rate CVs<0.3 yielded truncated r distributions; reproductive rate CVs>0.3 led to r distributions with long tails far beyond 1.5). The stochasticity introduced in natural mortality rates was subsequently propagated into the survival rate and expected survivorship-at-age.

For each replicate, the scalar number for the initial (year-1) population-at-age of female Atlantic Croaker was 1000. McAllister et al.'s (2001) Equations 9–14 or Hammond and Ellis' (2005) Equations 1–5 were applied as appropriate. During the sampling, there were negative values of r . These values usually result from generating stochastic reproductive rates and survivorship values independently of one another, including coupled low values of these parameters, the combination of which can lead to a population that cannot sustain itself (McAllister et al., 2001; Hammond and Ellis, 2005). The final prior probability density function for r (Table 1) was developed after discarding those negative r values and ensuring that the age structure of the projected population was stable (population stability occurred since year-3).

parameters are the asymptotic length (L_∞), the growth rate (K), and the theoretical age when length is zero (α_0). The parameters of the fecundity (number of eggs)–length relationship are the coefficient (β) and the exponent (γ).

Attribute	Value or range	Source
Age (a , years)	0–15+	ASMFC ¹
von Bertalanffy growth parameters:		ASMFC ¹
L_∞ (mm)	431	
K (mm×year ⁻¹)	0.214	
α_0 (years)	-2.35	
Fecundity (F)–length(L) relationship: $F = \beta L^\gamma$		Morse (1980)
β	0.002594179	
γ	3.361	
Maturity-at-age (ages: 0–15+ years)	0, 0.9, 1,.....	Barbieri et al. (1994)
Natural mortality-at-age (year ⁻¹ ; age: 0–15+)	0.461, 0.374, 0.324, 0.293, 0.272, 0.257, 0.246, 0.238, 0.232, 0.227, 0.223, 0.220, 0.218, 0.216, 0.215, 0.214	ASMFC ¹