Forecasting the dynamics of a coastal fishery species using a coupled climate–population model

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Abstract. Marine fisheries management strives to maintain sustainable populations while allowing exploitation. However, well-intentioned management plans may not meet this balance as most do not include the effect of climate change. Ocean temperatures are expected to increase through the 21st century, which will have far-reaching and complex impacts on marine fisheries. To begin to quantify these impacts for one coastal fishery along the east coast of the United States, we develop a coupled climate–population model for Atlantic croaker (*Micropogonias undulatus*). The model is based on a mechanistic hypothesis: recruitment is determined by temperature-driven, overwinter mortality of juveniles in their estuarine habitats. Temperature forecasts were obtained from 14 general circulation models simulating three CO_2 emission scenarios. An ensemble-based approach was used in which a multimodel average was calculated for a given CO_2 emission scenario to forecast the response of the population. The coupled model indicates that both exploitation and climate change significantly affect abundance and distribution of Atlantic croaker. At current levels of fishing, the average (2010–2100) spawning biomass of the population is forecast to increase by 60–100%. Similarly, the center of the population is forecast to shift 50–100 km northward. A yield analysis, which is used to calculate benchmarks for fishery management, indicates that the maximum sustainable yield will increase by 30–100%. Our results demonstrate that climate effects on fisheries must be identified, understood, and incorporated into the scientific advice provided to managers if sustainable exploitation is to be achieved in a changing climate.

Key words: abundance; Atlantic croaker; climate change; distribution; East Coast, USA; environmental effects; fishery management; Micropogonias undulatus; *population dynamics.*

Introduction

Overexploitation results in dramatic declines in marine population abundance and affects overall marine ecosystem structure. Fishing is often the dominant source of post-juvenile mortality for exploited species, causing direct reductions in population abundance (Myers et al. 1997, Christensen et al. 2003). Most fishing practices truncate the age and size distribution through increased mortality and size selectivity, which potentially reduces reproductive potential of the population because larger females may produce more and higher quality offspring (O'Farrell and Botsford 2006, Scott et al. 2006). Fishing also impacts marine ecosystems that support fisheries both directly, through the effects of fishing gear on habitats (Barnes and Thomas 2005, Reed et al. 2007), and indirectly, with the alteration of trophic pathways through the selective removal of species as targeted catch or bycatch (Jackson et al. 2001, Frank et al. 2005). Fisheries management strives to balance the exploitation of a select group of species against the sustainability of marine species and marine ecosystems, as well as the human communities and economic activity that fisheries and marine ecosystems support (NRC 1999, Hilborn et al. 2003).

Environmental variability and climate change also impact marine fisheries (Koster et al. 2003, Drinkwater et al. 2009). Recruitment, the process by which young fish join the adult or exploited population, is highly variable in most marine fish populations, largely as a result of environmental variability (Rothschild 1986). Growth and maturity rates are also affected by environmental variability including abiotic (e.g., temperature) and biotic (e.g., availability of food) factors (Brander 1995, Godø 2003). Yet most fisheries stock assessments, which form the scientific basis for fisheries management, do not include the effect of the environment on populations; environmental effects are assumed

to be the same in the future as in the past and thus are already reflected in the biological characteristics of the population (Richards and Maguire 1998, Hilborn and Walters 2004).

Climate change is resulting in long-term increases in temperature, changes in wind patterns, changes in freshwater runoff, and acidification of the ocean (IPCC 2007b, Doney et al. 2009). These changes are impacting the abundance, distribution, and productivity of fishery species directly (e.g., temperature effects on growth) and indirectly (e.g., changes in ocean productivity) (Stenseth et al. 2002, Perry et al. 2005). Long-term environmental change creates problems for fisheries stock assessment because the future environment will be different than the past. Previous estimates of population rates (growth, reproduction, recruitment) may not be appropriate for the future, and thus even well-intentioned fisheries management plans may fail because they do not account for climate-driven changes in the characteristics of exploited populations (NRC 1999, Kell et al. 2005, Kaje and Huppert 2007, Mackenzie et al. 2007, Rockmann et al. 2007).

Incorporating environmental effects in models for exploited fishery populations is not new (Hilborn and Walters 2004). Although correlative relationships are often used, numerous studies have indicated that to use environmentally explicit population models in forecasting (predicting the status of the population in the future based on environmental predictions) requires a mechanistic understanding of environmental forcing and population dynamics (Myers 1998, Krebs and Berteaux 2006, Hollowed et al. 2009). In the context of climate change, environment–population models have been developed for fisheries; for example, Atlantic cod abundance in the North Sea and the Gulf of Maine in the future is likely to be lower than currently assessed, raising the possibility of overexploitation even under management strategies designed to prevent overfishing unless target levels of exploitation are adjusted accordingly (Clark et al. 2003, Cook and Heath 2005, Fogarty et al. 2008). These studies demonstrate that climate effects on fisheries have important consequences for the long-term sustainability of exploited populations.

We examine the effect of climate change on Atlantic croaker (*Micropogonias undulatus*, Teleostei: Perciformes: Sciaenidae) based on a mechanistic recruitment hypothesis. Atlantic croaker is a coastal marine fish inhabiting the east coast of the United States (Murdy et al. 1997) that supports a fishery of ~8000 Mg with a value of approximately US$9 million (NMFS 2008). Atlantic croaker spawn pelagic eggs (~1 mm in diameter) in the coastal ocean during late summer, fall, and winter. Late larvae enter estuaries (e.g., Delaware Bay, Chesapeake Bay, Pamlico Sound) after 30–60 days in the plankton (Warlen 1982), and juveniles spend their first winter in estuarine nursery habitats (Able and Fahay 1998). Juvenile survival through the winter is determined by estuarine water temperatures; cold water leads to low survival, which in turn decreases recruitment to the population. This mechanistic recruitment hypothesis is supported by laboratory results (Lankford and Targett 2001a, b) and field observations (Norcross and Austin 1981, Hare and Able 2007).

We incorporate this hypothesis into a population model with recruitment as a function of spawning-stock biomass and minimum winter temperature. We then couple this population model with forecasts of minimum winter temperature from 14 general circulation models (GCMs) based on three CO_2 emission scenarios. We model the abundance, distribution, and yield of the population under different climate change scenarios and different fishing rates. We find that both climate and fishing affect the dynamics of the population and conclude that climate change will have major consequences for the Atlantic croaker population of the east coast of the United States in the coming decades.

MATERIALS AND METHODS

Climate models

The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (IPCC 2007b) included simulations from 23 different GCMs run with standardized CO_2 emission scenarios. Here we use 14 of these models (Table 1) and three emission scenarios: the commitment scenario, in which atmospheric CO_2 is fixed at 350 ppm through the 21st century; the B1 scenario, in which CO_2 increases to 550 ppm by the end of the 21st century; and the A1B scenario, in which CO_2 increases to 720 ppm by the end of the 21st century (IPCC 2007b). The 14 GCMs were chosen because the results are publically available for the three climate scenarios (commit, B1, and A1B) and for a retrospective analysis of the 20th century (IPCC Data Distribution Centre; *available online*).[6] Also, the models and scenarios included had simulations through 2100. Some of the models have more than one run for one or more of the climate scenarios; only one run was included for each model and scenario to ensure that the models were treated similarly. A comparison of retrospective 20th century analysis from each GCM and observed minimum winter air temperatures (1895–2007) was used to bias-correct the model results; mean of model outputs were compared to observations and the difference was added to minimum winter air temperatures forecast by the model (comparisons are provided in the Appendix: section 1).

Air temperature, which is forecast in most GCMs, is a good proxy for estuarine water temperatures owing to the efficient ocean–atmosphere heat exchange in estuarine systems (Roelofs and Bumpus 1953, Hare and Able 2007). Winter air temperature is also strongly coherent along the U.S. East Coast (Joyce 2002) and one location

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[6] ⟨http://www.mad.zmaw.de/IPCC_DDC/html/SRES_AR4/index.html⟩

TABLE 1. List of general circulation models (GCMs) used in this study and their associated modeling centers.

Modeling center	GCM
Bjerknes Centre for Climate Research, Norway	BCM2.0
Canadian Centre for Climate Modelling and Analysis, Canada	CGCM3 (T47 resolution)
Centre National de Recherches Meteorologiques, France	CM3
Australia's Commonwealth Scientific and Industrial Research Organisation, Australia	Mk3.0
Meteorological Institute, University of Bonn, Germany, Meteorological Research Institute of Korea Meteorological Administration, Korea, Model and Data Group at MPI-M, Germany	ECHO-G
Institute of Atmospheric Physics, China	FGOALS-g1.0
Geophysical Fluid Dynamics Laboratory, USA	CM2.1
Goddard Institute for Space Studies, USA	E-R
Institute for Numerical Mathematics, Russia	CM3.0
Institut Pierre Simon Laplace, France	CM4
National Institute for Environmental Studies, Japan	MIROC3.2 medres
Meteorological Research Institute, Japan	CGCM2.3.2
National Center for Atmospheric Research, USA	CCSM3
Met Office, UK	HadCM3

Notes: Three CO_2 emission scenarios from 14 GCMs were used. Data were obtained from the Model and Data Group at the Max-Planck-Institute for Meteorology (MPI-M) (see Appendix: section 1).

can be used as a proxy for a larger area (Appendix: section 1). Thus, minimum winter air temperature in the Chesapeake Bay region is used as the climate input into the coupled climate–population model. The Chesapeake Bay region was chosen because this estuary is a major Atlantic croaker overwintering nursery (Murdy et al. 1997, Able and Fahay 1998).

Population model

A finite time step model (Fogarty 1998, ASMFC 2005) was developed for the population of Atlantic croaker along the mid-Atlantic coast of the United States. Spawning-stock biomass (S) in a given year was calculated as the sum of the number of individuals (N) at each age (A) in that year (y) multiplied by a constant mass-at-age (W_A), a constant percentage mature-at-age (m_A), and a constant sex ratio (SR = 0.5):

$$S_y = \sum_A N_{Ay} \times W_A \times m_A \times \text{SR}. \qquad (1)$$

The values for W_A, m_A, and SR were taken from the most recent Atlantic croaker stock assessment (Table 2).

The mechanistic hypothesis that recruitment is determined by winter water temperatures affecting mortality during the juvenile stages was incorporated into the model using an environmentally explicit stock–recruitment relationship. In the model, numbers at age 1 in year y (N_{1y}) equaled recruitment in year y (R_y). Recruitment in year y was calculated based on spawning-stock biomass in year $y − 1$ (S_{y-1}) with the addition of the term for minimum winter temperature during year $y − 1$ (December) and year y (January, February, and March; denoted T_y):

$$N_{1y} = R_y = S_{y-1}\exp[a - bS_{y-1} + cT_y + \varepsilon]. \qquad (2)$$

This form of the stock–recruitment relationship was

used because it provided the best fit to observed data (Appendix: section 2). The climate effects on the population entered the model through the temperature term (T). Error in the stock–recruitment relationship (ε) was included formally in the model as a normally distributed random variable parameterized from the fit of the model to data.

Number-at-age in a given year (N_{Ay}) was calculated from number at the prior age in the prior year ($N_{(A-1)(y-1)}$) discounted by mortality, which was split into two components: fishing mortality (F) and natural mortality (M). Fishing mortality is an instantaneous rate used to calculate how many fish are removed from a population through fishing over a period of time. Natural mortality is similar but is used to calculate how many fish are removed from a population through natural causes (e.g.,

TABLE 2. Age-specific parameters used in the population model: mass-at-age (W_A), proportion mature-at-age (m_A), and proportional availability to fishing-at-age (s_A) for Atlantic croaker (*Micropogonias undulatus*).

Age	Parameter			
	W_A	m_A	s_A	N_{1900}
0	0.05	0	0.06	3.40×10^8
1	0.12	0.9	0.50	7.50×10^7
2	0.22	1.0	0.67	6.80×10^7
3	0.32	1.0	0.83	1.30×10^8
4	0.43	1.0	0.97	9.20×10^7
5	0.52	1.0	0.97	2.70×10^7
6	0.61	1.0	0.97	5.60×10^6
7	0.68	1.0	0.97	1.70×10^7
8	0.74	1.0	0.97	1.10×10^7
9	0.79	1.0	0.97	8.20×10^6
10+	0.83	1.0	0.97	1.70×10^7

Notes: These values were taken from the most recent stock assessment (ASMFC 2005). Also included are the numbers-at-age assumed for 1900 (N_{1900}), the first year of the simulations.

predation, disease) over a period of time. Fishing mortality was multiplied by an age-dependent selectivity coefficient (s_A; Table 2), because younger ages are less susceptible to capture in the fishery compared to older individuals:

$$N_{Ay} = N_{(A-1)(y-1)} e^{-(F s_{A-1} + M)}. \qquad (3)$$

The model was implemented for 1900 to 2100 using observed (1900–2007) and simulated (2008–2100) minimum winter air temperatures. Natural mortality (M) was assumed to be constant with a normally distributed random component ($\mu = 0.3$, $\sigma = 0.05$); this value was taken from the recent stock assessment (ASMFC 2005). For model hindcasts, historical fishing mortality rates (F) were set to levels consistent with the history of the fishery (Table 3). For model forecasts, rates of fishing (F) ranged from 0 to 1 with a random component ($\mu = 0$, $\sigma = 0.02$). For each climate scenario and GCM, 100 population simulations were calculated to include the variability associated with stochasticity in natural mortality (M), fishing mortality (F), and the unexplained variability in recruitment (ε).

The outputs from the coupled model were averaged over time (2010–2100), because GCMs do not produce annual predictions; i.e., due to random climate variability, a given year in the model is not expected to match that in nature. The 14 GCMs were treated as a multimodel ensemble (Reichler and Kim 2008): the results of the different GCMs were combined to make inferences about the effect of climate change on the Atlantic croaker population. Two approaches were used to evaluate the output of the coupled model: (1) the distribution of model results were compared to past estimates of spawning-stock biomass (1972–2004) and (2) a multimodel mean spawning-stock biomass was calculated for each climate scenario across all 14 GCMs. Our results represent the mean response of the Atlantic croaker population to several climate change scenarios over the 21st century for an ensemble of GCMs.

Distribution model

The mid-Atlantic croaker stock makes annual south-to-north migrations from wintering grounds off the Carolinas to summering grounds from North Carolina to New Jersey (Murdy et al. 1997). Atlantic croaker also exhibit onshore–offshore migrations from nearshore and estuarine areas in summer to coastal and shelf areas in fall (Murdy et al. 1997). We used a multiple-regression approach to model the mean distance and northern extent of the population as a function of spawning-stock biomass and the previous year's minimum winter temperature. Mean distance and northern extent estimates were calculated from data collected by the autumn trawl survey of the National Marine Fisheries Service (Azarovitz 1981; see Plate 1). This survey is based on a random stratified design, with multiple randomly located trawl stations in each stratum, which

TABLE 3. Time-specific fishing mortality rates (F) for Atlantic croaker used in the coupled climate–population model.

Years	F
1900–1934	0.2
1935–1944	0.3
1945–1954	1.3
1955–1964	0.8
1965–1984	0.6
1985–2005	0.2
2006–2015	linear between 0.2 and 2016 level
2016–2100	fixed at a level from 0 to 1 (0.1 step) with random annual component ($\mu = 0$, $\sigma = 0.02$)

Note: Values from 1900–2005 were used in the hindcasting portion of the model, and values from 2006–2100 were used in the forecasting portion of the model.

are defined by along-shelf regions and bathymetric zones (Azarovitz 1981).

Since the northeast U.S. shelf does not run simply north–south, a curvilinear grid of distance from Cape Hatteras, North Carolina, was developed; the grid approximately followed the 10-m isobath. This grid was then used to convert each stratum's mean location (latitude and longitude) to a strata average along-shelf distance from Cape Hatteras. Using mean catch in each strata and mean distance to each strata, we calculated a weighted-mean distance for Atlantic croaker in each year. We also calculated weighted standard deviation of distance. Based on the idea that range expands at higher population sizes (MacCall 1990) and the suggestion that summer distribution may be influenced by temperatures during the previous winter (Murdy et al. 1997), we developed an empirical model for mean location (dist$_\mu$) and its standard deviation (dist$_\sigma$), based on spawning-stock biomass (S) and temperature (T):

$$\text{dist}_{\mu_Y} = a_\mu + b_\mu S_Y + c_\mu T_Y + d_\mu S_Y^2 + e_\mu T_Y^2 \qquad (4)$$

$$\text{dist}_{\sigma_Y} = a_\sigma + b_\sigma S_Y + c_\sigma T_Y + d_\sigma S_Y^2 + e_\sigma T_Y^2. \qquad (5)$$

All potential variations of the above models were fit ($y = a + bS$; $y = a + cT$; $y = a + bS + cT$; etc.) and compared using the Akaike Information Criteria. Evaluation of Akaike weights indicated that several models were equally supported, and thus we chose to use a multimodel inference procedure (Burnham and Anderson 1998) to determine the parameters of the statistical model (a, b, c, d, and e). The final empirical model explained 31% and 37% of the variability in the mean and standard deviation of the annual center of the population. A logistic regression approach also was developed (Appendix: section 3); the results were similar so we only present the results of the multiple regression model.

For distribution forecasts, spawning-stock biomass estimates from the coupled climate–population model were combined with minimum winter temperature estimates from the GCM scenarios. The outputs from the distribution model were averaged over the period of

PLATE 1. A basket of Atlantic croaker (*Micropogonias undulates*) collected during the 2009 Northeast Fisheries Science Center Autumn Bottom Trawl Survey aboard the NOAA Ship *Henry B. Bigelow*. These surveys document the abundance and distribution of fishes and macro-invertebrates on the northeast U.S. continental shelf. In addition to identifying the catch, a number of individual-level parameters are measured for many species, including length, weight, maturity, age, and diet. These data are used in a wide variety of assessments and research studies. Oceanographic and plankton data are also collected and used to examine links between fish and invertebrate populations and environmental and oceanographic forcing. Photo credit: Keiichi Uchida.

2010–2100, similar to the results of the population model. We used the mean and standard deviation models to forecast the mean and northern extent of the population; the latter was defined as the mean plus two standard deviations. In addition to mean center of the distribution and mean northern extent, the frequency of years with the northern extent past the Hudson Canyon was quantified. Historically, Hudson Canyon is near the absolute northern limit of the population and is an important geographic feature on the northeast U.S. continental shelf separating the mid-Atlantic region from the Southern New England region (Sherman 1980).

Using data from the autumn trawl survey is potentially biased by the timing of the fall migration; as waters cool, adult Atlantic croaker move south (Murdy et al. 1997, Able and Fahay 1998). Thus, the timing of the survey relative to the timing of the fall migration confounds the ability to compare distribution among years. Assuming the fall migration is triggered by temperature, we screened shelf temperatures observed during each annual survey. There were several years (5 of 33) in which temperatures off New Jersey were cooler than most other years (e.g., <17°C), indicating that fall cooling started earlier in these years. These cooler years were removed from the analysis in an attempt to compare the distribution of Atlantic croaker at the same point in the seasonal cycle.

Yield analysis

We estimated the fishing rate threshold and yield target under current conditions and under the three CO_2 emission scenarios based on the temperature-dependent recruitment model. The purpose was to calculate management benchmarks for the population under the different climate change scenarios. The environmentally explicit stock–recruitment relationship (Eq. 2) can be linearized:

$$\log_e\left[\frac{R_y}{S_{y-1}}\right] = \log_e a - bS_{y-1} + cT_y. \qquad (6)$$

Solving for spawning-stock biomass (S) results in:

$$S_{y-1} = \frac{1}{b}\left\{\log_e\left[a\left(\frac{S_{y-1}}{R_y}\right)\right] + cT_y\right\}. \qquad (7)$$

Note that the expression inside the brackets includes spawning biomass-per-recruit (S/R). Given estimates of the parameters of the recruitment models and standard yield and spawning biomass-per-recruit analyses (Lawson and Hilborn 1985, Quinn and Desiro 1999), estimates of S/R are substituted for different levels of fishing mortality (here designated as $(S/R)_F$) to determine the total spawning biomass for each fishing mortality rate. Once the total spawning biomass corresponding to a particular level of fishing mortality (S_F) was determined, the corresponding recruitment was obtained by the following simple identity:
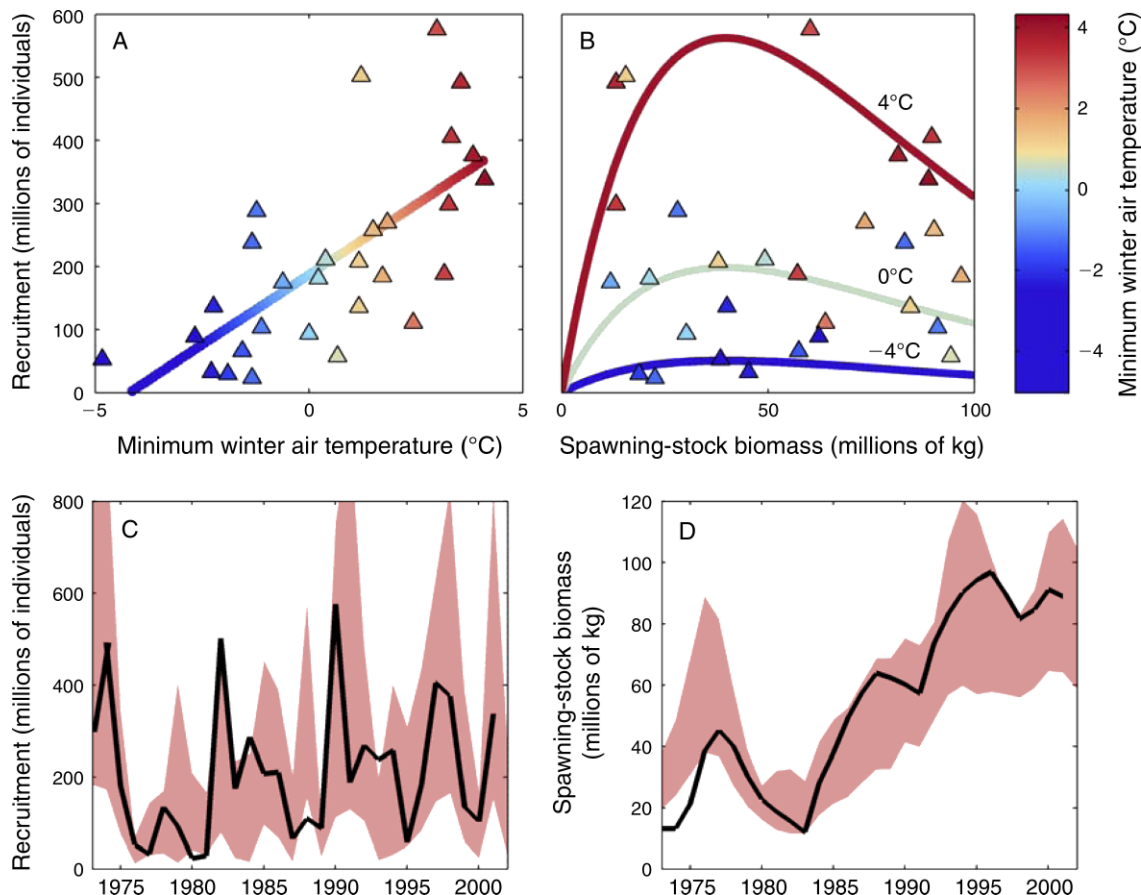
Fig. 1. Relationship between Atlantic croaker (*Micropogonias undulatus*) recruitment and minimum winter air temperature along the mid-Atlantic coast of the United States and comparison of observed recruitment and spawning-stock biomass with hindcasts developed from a coupled climate–population model. (A) Relationship between minimum winter air temperature in Virginia, USA, and recruitment of Atlantic croaker ($r = 0.68$, $P < 0.001$). (B) Environmental stock–recruitment relationship for Atlantic croaker ($r^2 = 0.61$, $P < 0.001$). The environmental stock–recruitment function yields a three-dimensional surface, with spawning-stock biomass, minimum winter temperature, and recruitment as the three dimensions. To visualize this surface in two dimensions, estimates of recruitment are shown for three fixed temperatures (−4°C, 0°C, and +4°C). (C, D) Comparison of observed and modeled recruitment and spawning-stock biomass from 1973 to 2003 based on the coupled climate–population model. Observed values (black lines) are from the stock assessment (ASMFC 2005). Modeled values are shown as the mean ± SD of 100 runs of the coupled climate–population model (red shading).

$$R_F = \frac{S_F}{(S/R)_F}. \qquad (8)$$

The equilibrium yield for each level of fishing mortality was obtained by combining the yield per recruit at each level of fishing mortality with this predicted recruitment level to obtain an estimate of the total yield at each level of fishing mortality:

$$Y_F = (Y/R)_F R_F. \qquad (9)$$

The fishing rate at maximum sustainable yield (F_{MSY}) is defined as the F resulting in the maximum sustainable yield (MSY = max(Y_F)). These equations were applied to the average S and R forecasts for each climate scenario resulting is MSY and F_{MSY} for each climate scenario.

RESULTS

Environmentally explicit stock–recruitment relationship

Observed recruitment of Atlantic croaker in the mid-Atlantic region is significantly correlated to minimum winter air temperature (Fig. 1A), strongly supporting the mechanistic recruitment hypothesis. Including a temperature term in the stock–recruitment model provides a significantly better fit compared to including spawning-stock biomass alone (Appendix: Table A4) and explains 61% of the variance in recruitment (Fig. 1B). Including temperature in the stock–recruitment relationship permitted the detection of a significant compensatory population effect (e.g., a dome-shaped stock–recruitment function) that was masked by temperature-driven variability. Simulated recruitment and spawning-stock biomass largely overlapped with recruit-
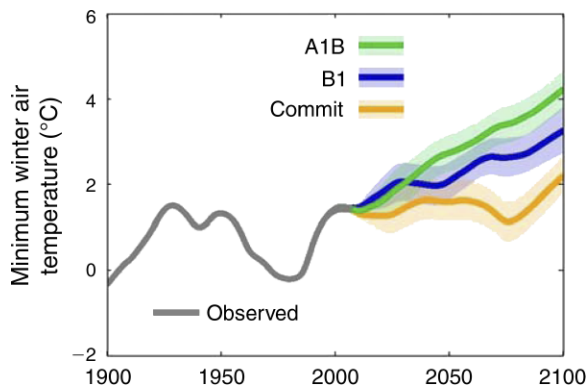
FIG. 2. Observations and general circulation model (GCM) projections of minimum winter air temperature in the Chesapeake Bay region from 1900 to 2100. Results from three CO_2 emission scenarios (A1B, B1, and commit) averaged for 14 GCMs are shown. Long-term trends in temperature are represented by a 30-point lowess smoother fit to the annual series; these smoothed trends included a combination of observed and modeled temperatures so the divergence between observations and models occurs prior to the end of the observations. Lines represent the multimodel mean of the GCMs, and shading represents 95% confidence intervals. See *Materials and methods: Climate models* for an explanation of the CO_2 emission scenarios.

ment and spawning-stock biomass from the stock assessment (ASMFC 2005), providing confidence that the model captures the large-scale dynamics of the population (Fig. 1C, D).

Minimum winter temperatures

As the level of atmospheric CO_2 increases, GCMs predict that minimum winter temperatures in the Chesapeake Bay region of the United States will increase (Fig. 2). Under the commit scenario (CO_2 constant at 350 ppm), the models predict little trend in minimum winter temperatures; fluctuations are dominated by natural variability within the climate system. In contrast, under the B1 and A1B scenarios, the models predict increasing minimum winter air temperatures with values higher than observed during the 20th century.

Population abundance

With increasing minimum winter temperatures, the coupled climate–population model predicts that Atlantic croaker abundance will increase (Fig. 3). Increased temperatures result in higher recruitment, which leads to higher spawning-stock biomass. At current levels of fishing mortality ($F = 0.11$), all GCMs and all scenarios predicted higher population abundances than observed since the early 1970s (when estimates of spawning-stock biomass started). Ensemble mean increases in spawning-stock biomass of 63%, 82%, and 92% are projected under the commit, B1, and A1B scenarios, respectively. Fishing also influences abundance; as fishing mortality increases, spawning-stock biomass decreases. Forecasted spawning-stock biomass decreases as fishing mortal-

ity increases, counteracting the effect of warming, but even at higher fishing mortality rates ($F = 0.4$), all GCMs for the B1 and A1B scenarios predict higher population abundances than observed in the past. These results are intuitive based on the structure of the model and the relationship between temperature and recruitment, but unless fishing mortality increases by more than fourfold, the coupled population–climate model indicates that Atlantic croaker biomass will increase in the future.

The model also allows the effect of climate change on population dynamics to be quantified relative to the effect of fishing through the comparison of the partial derivatives of spawning-stock biomass (S) relative to climate scenario (C) ($\partial S/\partial C$) and fishing (F) ($\partial S/\partial F$)
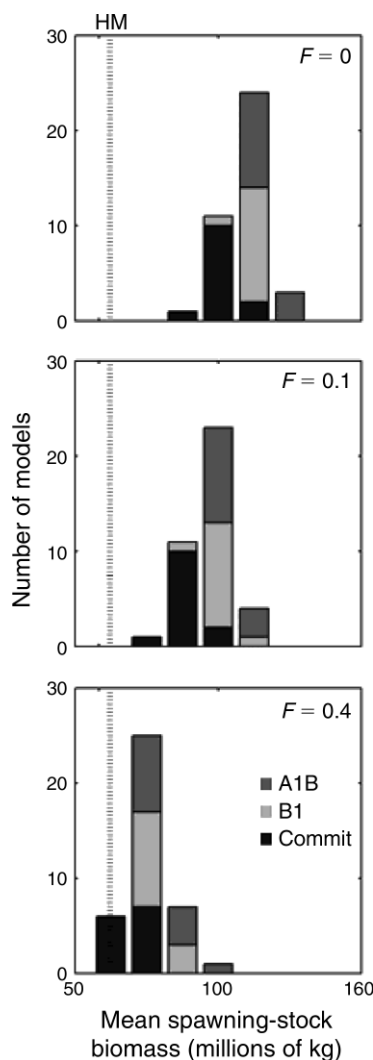

FIG. 3. Forecasts of the effects of climate change on Atlantic croaker spawning-stock biomass for each of 14 general circulation models (GCMs) and three CO_2 emission scenarios (A1B, B1, and commit) at three fishing mortalities ($F = 0$, $F = 0.1$, and $F = 0.4$). Historical means (HM) of spawning-stock biomass are shown (1972–2004).
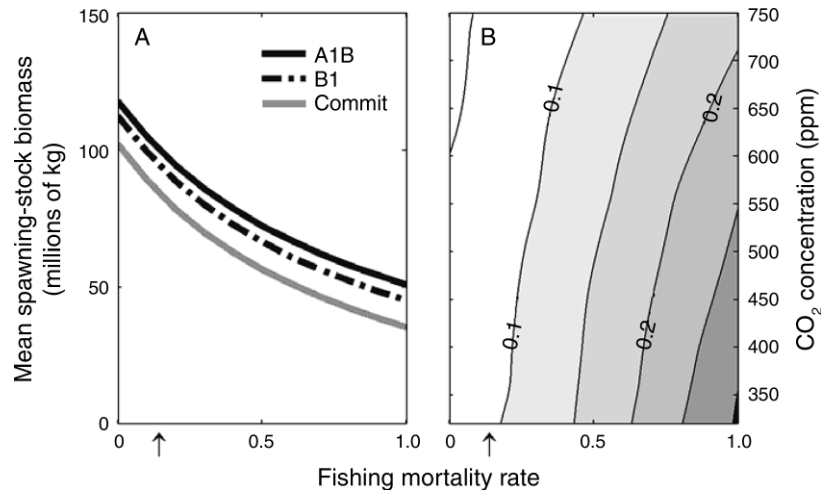
FIG. 4. (A) Ensemble multimodel mean spawning-stock biomass (2010–2100) for three climate scenarios (A1B, B1, and commit) and a range of fishing mortality rates for Atlantic croaker. (B) Contours of $(\partial S/\partial C)/(\partial S/\partial F)$, which is a measure of the relative effect of climate compared to fishing on spawning-stock biomass (see *Results: Population abundance*). Arrows along the x-axis indicate the current fishing mortality rate.

(Fig. 4). As fishing mortality rate increases, $\partial S/\partial F$ decreases. In contrast, $\partial S/\partial C$ remains relatively constant over the range of fishing mortality rates. As a result, at lower fishing mortality rates, the effect of climate is 10–20% of the effect of fishing, while at higher fishing mortality rates, the effect of climate is 20–30% of the effect of fishing. In other words, an increase in atmospheric CO_2 from 350 to 550 ppm is approximately equivalent to a 0.2 decrease in fishing mortality rate. This is a substantial effect given that the estimated range of fishing mortality on Atlantic croaker was 0.03–0.49 from 1973 to 2002 (ASMFC 2005).

Population distribution

The empirical distribution model predicts that with increasing minimum winter air temperatures, the range of Atlantic croaker will expand northward. Fishing also has a strong effect on distribution, because fishing mortality affects spawning-stock biomass (Fig. 5). At zero fishing mortality, all climate models and scenarios forecast a northward shift in the population of 50–200 km; the shift is greater at higher levels of atmospheric CO_2. Likewise, the northern extent of the distribution is forecast to shift 100–400 km northward, and the frequency north of Hudson Canyon increases 10–40%, depending on the GCM and CO_2 emission scenario. As fishing mortality increases to 0.1 (the current level) and 0.4, the range expansions are predicted to be less. At current levels of fishing (0.1), however, all B1 and A1B scenarios and most commit scenarios forecast a northward expansion of range. At relatively high fishing mortality rates (0.4), most models predict no change in mean distribution and frequency north of Hudson Canyon and only a modest increase in the northern extent of ~50 km.

The ensemble means exhibit the same patterns as described above: with increased atmospheric CO_2 and resulting warming, the Atlantic croaker population will expand northward if fishing remains at recent levels (Fig. 6). The population is predicted to move 50–100 km northward during the 21st century if fishing remains near 0.1; the northern limit of the population is predicted to shift 75–175 km northward. Further, interannual variability is predicted to extend the northern limit of the population past Hudson Canyon in 10–30% of the years from 2010 to 2100. Over the past decade, Atlantic croaker has become a regular fishery species in Delaware Bay and coastal New Jersey, and our results indicate that this trend will continue and that Atlantic croaker will be observed more frequently in waters of southern New England in the coming decades.

Population yield

A yield analysis based on the coupled climate–population model estimates that management benchmarks for Atlantic croaker in the mid-Atlantic region will change dramatically with increasing minimum winter air temperatures. Fishery benchmarks are biological reference points based on exploitation characteristics of the population that are used for guidance in developing fishery management strategies (Restrepo et al. 1998). For Atlantic croaker, thresholds and targets for fishing rate and spawning-stock biomass have been defined relative to an estimated MSY and to the fishing mortality rate (F_{MSY}), which, if applied constantly, would result in MSY (ASMFC 2005). Based on ensemble averages across all GCMs, F_{MSY} and MSY increase under all three climate scenarios compared to estimates based on mean minimum winter air temperatures over the past 30 years (Fig. 7). The yield curve flattens at higher fishing mortality rates, so comparing
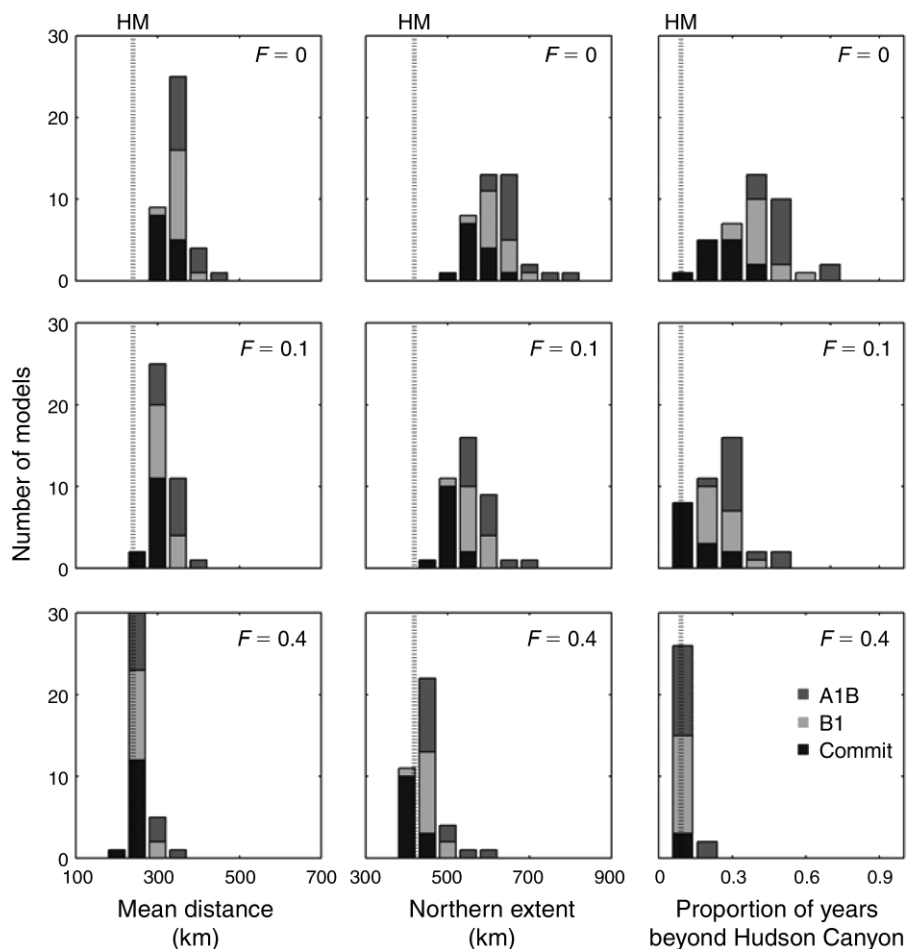
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Fɪɢ. 5. Forecasts of the effect of climate change on Atlantic croaker distribution in the mid-Atlantic region of the northeast U.S. continental shelf. Mean location, northern extent, and frequency north of Hudson Canyon are shown based on three CO_2 emission scenarios (A1B, B1, and commit) and from 14 general circulation models (GCMs) at three fishing mortalities ($F = 0$, $F = 0.1$, and $F = 0.4$). Historical mean (HM) of distribution measures are shown (1972–2004).

F_{MSY} is somewhat arbitrary (a range of Fs result in similar yields), but forecasted MSYs are 35%, 73%, and 96% higher under the commit, B1, and A1B climate scenarios, respectively, compared to the estimated MSY based on observed minimum winter temperatures over the past 30 years (Table 4).

DISCUSSION

We conclude that both fishing and climate change impact the abundance and distribution of Atlantic croaker along the mid-Atlantic coast of the United States. Climate change also affects benchmarks used in fisheries management; MSY and F_{MSY} increase with increasing temperatures. Thus, benchmarks for the mid-Atlantic stock of Atlantic croaker set without consideration of climate change would be precautionary (Restrepo et al. 1998). The mid-Atlantic region represents the northern limit of Atlantic croaker, and we forecast that projected temperature increases will have positive effects on the species in this region (increased abundance and range), not considering other effects of climate change and ocean acidification (Doney et al. 2009, Drinkwater et al. 2009). For species with populations at the southern end of the distribution, similar modeling has forecast opposite results. For example, Atlantic cod is predicted to shift northward, becoming expatriated from the southern New England shelf. Further, the productivity of the cod fishery in the Gulf of Maine is predicted to decrease (Fogarty et al. 2008). In the instance of Atlantic cod, benchmarks used in management may be set too high, and this may lead unknowingly to unsustainable management practices even under stringent rebuilding plans (Fogarty et al. 2008). This contrast illustrates that in any region, some species will be positively affected by climate change, while others will be negatively affected. Further, climate change will affect the benchmarks used in fisheries management. Understanding and quantifying the effect of climate change on populations in combination with the effect of exploitation is a major challenge to
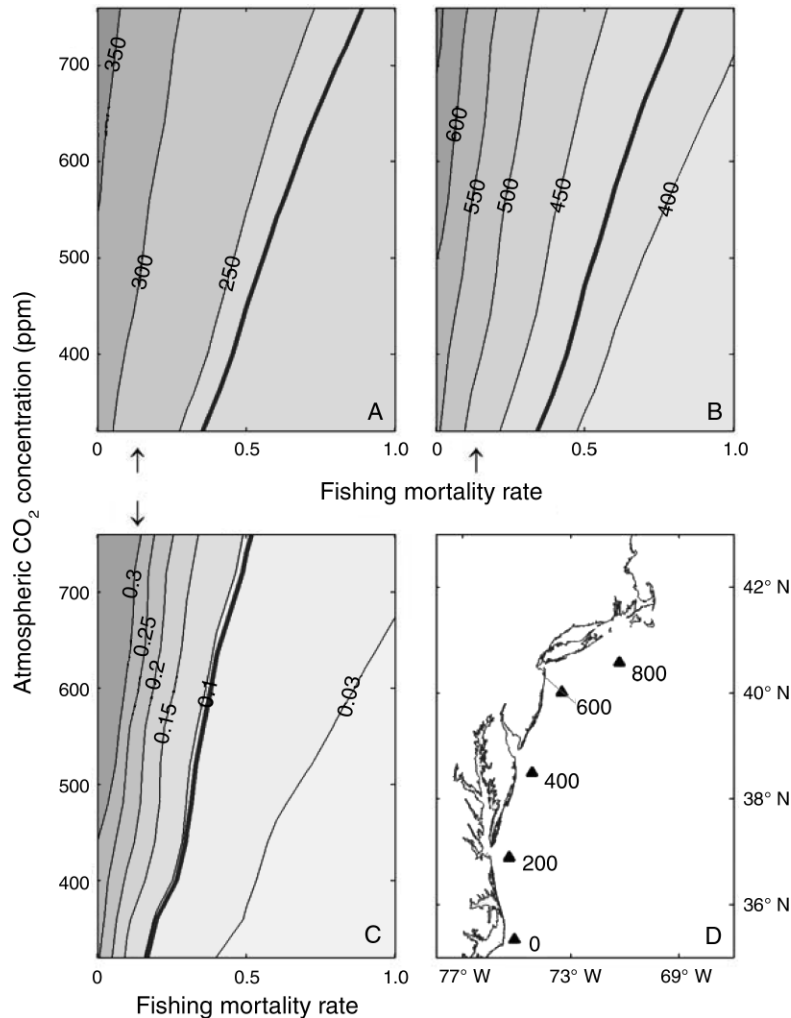
FIG. 6. (A) Ensemble multimodel mean Atlantic croaker population location, (B) northern extent of the range (mean + 2 SD), and (C) proportion of years when northern extent of the population is north of the Hudson Canyon (distance 600 km). (D) Maps of various distance marks along the continental shelf. The historical values (1972–2004) of mean location (~240 km), northern extent (~420 km), and proportion of years with the measure of northern extent exceeding 600 km (0.09) are shown as dark gray contours. Arrows along the x-axis indicate the level of current fishing mortality rate.

rebuilding and maintaining sustainable fisheries in the coming decades.

The coupled climate–population model developed here does not include all the potential climatic effects on Atlantic croaker. The population model has a number of parameters, all of which are potentially affected by warming temperatures: recruitment (included here), mass-at-age, maturity-at-age, natural mortality, fishing mortality, and catchability. The mass-at-age and maturity-at-age schedules could be linked to temperature (Brander 1995, Godø 2003). Natural mortality is included as a constant, but climate change may result in temporally variable predation pressure (Overholtz and Link 2007). Fishing mortality also may vary as fishing communities adapt to climate change (e.g., Hamilton and Haedrich 1999, Berkes and Jolly 2001, McGoodwin 2007), and catchability may change

as the population shifts northward, where trawl fisheries become more prevalent (Stevenson et al. 2004).

In addition to added climate effects in the population model, there are also different forms of models that could be used. Keyl and Wolff (2008) reviewed environmental–population models in fisheries and found six dominant types: stock–recruit analysis, surplus production models, age- or size-structured models, trophic and multispecies models, individual-based models, and generalized additive models. The population model used here for Atlantic croaker was an age-structured model with minimum winter temperature in year y and spawning-stock biomass in year y influencing recruitment in year $y + 1$. Time lags are built into this model since spawning-stock biomass is summed over age classes, the sizes of which are dependent on initial recruitment and subsequent mortality. Time lags also
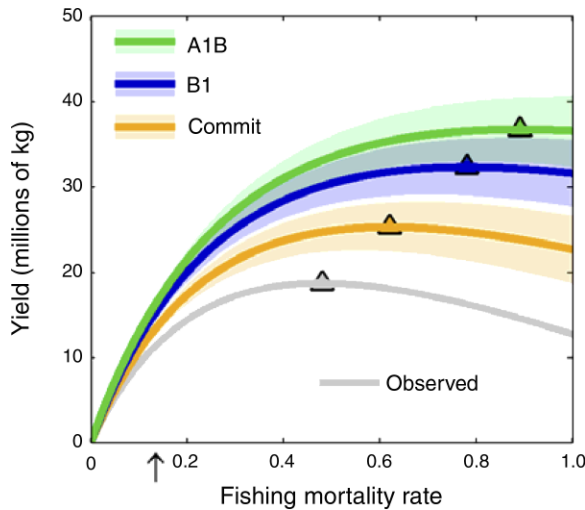
Fig. 7. Atlantic croaker fishery yield as a function of fishing mortality rate based on the temperature-dependent stock–recruitment model and ensemble multimodel mean of three climate scenarios (A1B, B1, and commit). Yield curves are presented as lines; maximum sustainable yields (MSY) and fishing rates at maximum sustainable yields (F_{MSY}) are indicated by triangles. Shading indicates 95% confidence intervals around multimodel mean.

could be incorporated through temperature-dependent growth (mass-at-age) or maturity functions. The distribution model used spawning-stock biomass in year y and minimum winter temperature in year $y - 1$ to predict distribution in year y. Similar to the population model, time lags are incorporated into the distribution model through the inclusion of spawning-stock biomass. Since Atlantic croaker is a migratory fish, it is also possible that migrations in previous years affect the distribution in the current year, resulting in additional time lags that are not considered in the current effort.

Although our model does not include all the potential complexities, it is based on a mechanistic recruitment hypothesis that is supported by both laboratory work (Lankford and Targett 2001a, b) and fieldwork (Norcross and Austin 1981, Hare and Able 2007). Further, the model is consistent with current fishery population models (Hilborn and Walters 2004) and represents one of the first attempts to link an ensemble of GCMs to a fish population model for use in fisheries management. The current model explains 61% of the variability in recruitment (Fig. 1B), 31% of the variability in distribution, and predicts the general patterns of spawning-stock biomass over the last 30 years (Fig. 1D). Additionally, the outputs from 14 GCM models are all consistent, and thus we have confidence in our long-term forecasts.

It is important to note that our effort examines Atlantic croaker at the northern part of its range (ASMFC 2005). The recent assessment considers two stocks of Atlantic croaker along the east coast of the United States: a northern stock (considered here) and a

southern stock (not considered). There is evidence that abundance of the southern stock is decreasing: catch has decreased in southern states and a fishery-independent abundance index of the southern stock has decreased (ASMFC 2005). These findings are consistent with the hypothesis that the southern stock is declining and withdrawing northward in response to climate change, but this question has not been examined in detailed and there has been little research of environmental influences on the dynamics of Atlantic croaker in the southern part of the range.

Our forecasts are on a 50- to 100-year scale. Fisheries management does not operate on these scales and shorter-term forecasts are required. The climate modeling community is focusing great effort on developing decadal-scale forecasts that include both externally forced changes (e.g., CO_2 emissions) and internal variability (e.g., Atlantic meridional overturning circulation, El Niño–Southern Oscillation) (Smith et al. 2007, Keenlyside et al. 2008). In the future, a range of climate forecasts of the status of fish populations (5–20 years, 20–50 years, 50–100 years) could be provided to scientists, managers, and fishers (Brander 2009). However, these forecasts need to include the effects of both fishing and climate on population dynamics (Planque et al. 2009).

Quantitative coupled climate–population models for fishery species are tractable, now, under certain circumstances. In the specific example, the climate–population link (survival of overwintering juveniles in shallow estuarine systems) is direct and well-reproduced by current climate models. Winter temperature is an important regulatory factor in many fish populations (Hurst 2007), and the effort here could be easily extended to some of these species. Climate–population links for many other species will be complicated and involve processes that cannot be simply indexed by air temperature. To develop climate–population models in these instances, climate models need to represent mechanistic hypotheses linking the regional oceanic

TABLE 4. Fishing rate at maximum sustainable yield (F_{MSY}), ensemble mean maximum sustainable yield (MSY), and 95% confidence interval on MSY for Atlantic croaker based on three CO_2 emission scenarios simulated with 14 general circulation models (GCMs).

Scenario	F_{MSY}	MSY (kg)	Confidence intervals (kg)
A1B	0.89	3.67×10^7	3.30–4.07×10^7
B1	0.78	3.23×10^7	2.90–3.58×10^7
Commit	0.62	2.52×10^7	2.24–2.82×10^7
Observed (1970-2002)	0.48	1.87×10^7	

Notes: Also provided are the values based on the most recent stock assessment of Atlantic croaker (ASMFC 2005); the values presented here are slightly different from those presented in the assessment because the model form used here (an environmentally explicit Ricker stock–recruitment function) is different from that used in the stock assessment (a standard Beverton-Holt function).

environment to population dynamics and ultimately include the interactions between populations and species (Winder and Schindler 2004, Helmuth et al. 2006, Cury et al. 2008). The development of such coupled models will contribute to the goal of providing the best scientific advice for managing fisheries in a future of changing climate (Perry et al. 2009), as well as to future assessments of the effect of climate change on regional resources, ecosystems, and economies(IPCC 2007a).

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APPENDIX

Background on general circulation models, choice of a stock–recruitment function, and distribution model based on logistic regression (*Ecological Archives* A020-012-A1).