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 since 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 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 two global climate models simulating three standard climate scenarios. The coupled climate-population model demonstrates that both exploitation and climate change will significantly affect abundance and distribution of Atlantic croaker in the future. 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 northwards. A yield analysis, which is used to calculate benchmarks for fishery management, indicates that the maximum sustainable yield will increase by 20-100%. Our results demonstrate that to achieve optimum exploitation of fishery resources in the face of changing climate, it is imperative that climate effects on fisheries are identified, understood, and incorporated into the scientific advice provided to managers.

KEYWORDS: Climate change, fishery management, population dynamics, fishery benchmarks, population abundance, population distribution

Introduction

Overexploitation results in dramatic declines in marine population abundance and affects overall marine ecosystem structure. Fishing is often the dominant source of mortality for exploited species causing direct reductions in population abundance (Myers et al. 1997, Christensen et al. 2003). Most fishing practices also truncate the age and size distribution through increased mortality and size-selectivity, which reduces reproductive potential of the population since larger females 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 communities and economic activity that fisheries support (Hilborn et al. 2003).

Environmental variability and climate change also impact marine fisheries (Koster et al. 2003). 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; there is an implicit assumption that environmental effects in the future will be the same as in the past and 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 affects 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 since 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 (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), but numerous studies have indicated that to use such models in forecasting (predicting the status of the population in the future based on environmental predictions), requires a mechanistic understanding between environmental forcing and population dynamics (Myers 1998, Krebs and Berteaux 2006). 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 (Clark et al. 2003, Cook and Heath 2005, Fogarty et al. 2007). These studies demonstrate that climate effects on fisheries have important consequences for the long-term sustainability of exploited populations.

Here we examine the effect of climate change on Atlantic croaker (*Micropogonias undulatus*, Pisces: 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 approximately 9,000 metric tons with a value of approximately 8 million dollars (National Marine Fisheries Service 2008). Atlantic croaker spawn pelagic eggs (~ 1mm 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 global climate models based on three standard 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 Intergovermental Panel on Climate Change (IPCC) (IPCC 2007b) included simulations from 23 different global climate models all run with standardized CO_2 emission scenarios. Here we use two of these models (GFDL Climate Model 2.1 and NCAR Community Climate System Model 3.0, (Delworth et al. 2006, Meehl et al. 2007)) and three emission scenarios (commitment scenario in which atmospheric CO_2 is fixed at 350 ppm through the 21st century, and the B1 and A1B scenarios in which CO_2 increases to 550 ppm, and 720 ppm, respectively, by the end of the 21st century (IPCC 2007b)). A comparison of climate model hindcasts and observed minimum winter air temperatures is included in Section 1 of the online Appendix. Results from both the GFDL and NCAR model were qualitatively similar, so only results from the GFDL model are shown; results of the NCAR model are provided in Section 4 of the online Appendix.

Air temperature, which is forecast in global climate models, 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 can be used as a proxy for a larger area (see Section 1 of online Appendix). 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 since this estuary is a major Atlantic croaker overwintering nursery (Murdy et al. 1997, Able and Fahay 1998).

Population Model – A finite time step population 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 weight-at-age (W_A), a constant percent mature at age (M_A), and a constant sex ratio (SR=0.5).

$$S_y = \sum_A N_{Ay} \cdot W_A \cdot M_A \cdot SR \qquad (1)$$

The values for W_A, M_A, and SR were taken from the most recent Atlantic croaker stock assessment (Table 1).

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 $y-1$ (Dec) and year y (Jan, Feb, and Mar) (denoted T_y).

$$N_{1y} = R_y = aS_{y-1}e^{(-b \cdot S_{y-1} + c \cdot T_y + \varepsilon)} \qquad (2)$$

This form of the stock-recruitment relationship was used on the basis that it provided the best fit to observed data (see Section 2 of the online Appendix). The climate effects on the population entered the model through the temperature term (T). Error in the stock recruitment relationship (ε) was formally included 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 spilt 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 used to calculate how many fish are removed from a population through natural causes (e.g., predation, disease) over a period of time. Fishing mortality was multiplied by an age-dependent selectivity coefficient (s_A, Table 1) (ASMFC 2005), since younger ages are less susceptible to capture in the fishery compared to older individuals.

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

The model was implemented for 1900 to 2100 using blended 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 (μ=0.3, σ=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 2). For model forecasts, rates of fishing (*F*) ranged from 0 to 1 with a random component (μ=0, σ=0.02). For each climate scenario, 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), since global climate models do not produce annual predictions. Thus, our results represent the mean response of the Atlantic croaker population to several climate change scenarios over the 21st century.

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). The survey is based on a random stratified design, with multiple randomly located trawl stations in each strata, which are defined by along-shelf regions and bathymetric zones (Azarovitz 1981).

Since the northeast U.S. shelf is non-linear, 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 strata average location (latitude and longitude) to a strata average along-shelf distance from Cape Hatteras. Using average catch in each strata and average 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).

$$dist_{\mu Y} = a_u + b_u S_Y + c_u T_Y + d_{\mu} S_Y{}^2 + e_u T_Y{}^2 \tag{4}$$

$$dist_{\sigma_Y} = a_{\sigma} + b_{\sigma} S_Y + c_{\sigma} T_Y + d_{\sigma} S_Y{}^2 + e_{\sigma} T_Y{}^2 \tag{5}$$

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 choose to use a multi-model 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 the annual center and northern extent of the population. A logistic regression approach also was developed (see Section 3 of the online Appendix); 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 global climate model scenarios. The outputs from the distribution model were averaged over the period of 2010-2100, similar to the results of the population model. In addition to mean center of the distribution and mean northern extent, the frequency of years with the northern extent past the New York apex were quantified; historically this is near the absolute northern limit of the population.

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 the shelf temperatures observed during each annual survey. There were several years where temperatures off New Jersey were cooler than most other years (e.g., $<17^{o}$C) and these 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 climate scenarios based on the temperature-dependent recruitment model. The purpose was to calculate the management benchmarks for the population under the different climate change scenarios. The environmentally explicit stock-recruitment relationship (equation 2), can be linearized:

$$\log_e\left[\frac{R}{S}\right] = \log_e a - bS + cT \qquad (6)$$

Solving for spawning stock biomass (S) results in:

$$S = \frac{1}{b}\left\{\log_e\left[a\left(\frac{S}{R}\right)\right] + cT\right\} \qquad (7)$$

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 (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 simple identity.

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

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, r=0.68, p<0.001), 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 (Table A2 in the online Appendix), and explains 61% of the variance in recruitment (Fig. 1B). Using the coupled climate-population model and historical temperatures shows that simulated recruitment and spawning stock biomass largely overlapped with spawning stock biomass and recruitment from the stock assessment (ASMFC 2005) providing confidence that the model captures the dynamics of the population (Fig. 1C and 1D).

Minimum winter temperatures - As the level of atmospheric CO_2 increases, the Geophysical Fluid Dynamics Laboratory (GFDL) Climate Model 2.1 predicts that minimum winter temperatures in the Chesapeake Bay region of the United States will increase. Under the commit scenario (CO_2 constant at 350 ppm), the GFDL model predicts little trend in minimum winter temperatures; fluctuations are dominated by natural variability within the climate system (Fig. 2). In contrast, under the B1 (CO_2 increasing to 550 ppm by 2100) and A1B (CO_2 increasing to 720 ppm by 2100) scenarios, the GFDL model predicts increasing minimum winter air temperatures with values higher than observed during the 20th century (Fig. 2).

Population abundance - With increasing minimum winter temperatures, the coupled climate-population model predicts that Atlantic croaker abundance will increase (Fig. 3A). Increased temperatures result in higher recruitment, which leads to higher spawning stock biomass. Comparing historical levels (1973-2004) to projected levels of spawning stock biomass, the coupled climate-population model predicts increases of 62%, 85% and 108% under the commit, B1, and A1B scenarios, assuming fishing mortality remains constant in the future. This result is intuitive based on the structure of the model and the relationship between temperature and recruitment. However, the model allows the effect of climate change on population dynamics to be quantified relative to the effect of fishing through comparison of the partial derivatives of spawning stock biomass (S) relative to temperature(T) ($\frac{\partial S}{\partial T}$, the difference is S among climate scenarios) and fishing (F) ($\frac{\partial S}{\partial F}$, the difference in S over a range of fishing mortality rates). As fishing mortality rate increases, $\frac{\partial S}{\partial F}$ decreases (Fig 3A). In contrast, $\frac{\partial S}{\partial T}$ remains relatively constant over the range of fishing mortality rates (Fig. 3A). 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 (Fig 3B). In other words, a 1^{o}C increase in minimum winter air temperature is approximately equivalent to 0.2 decrease in fishing mortality rate. This is a substantial effect given that the estimated range of fishing rate on Atlantic croaker was 0.03 to 0.49 from 1973-2002 (ASMFC 2005).

Population distribution - An empirical distribution model predicts that with increasing minimum winter air temperatures, the range of Atlantic croaker will expand northward (Fig. 3C, D, E). Fishing also has a strong effect on distribution, since fishing mortality affects spawning stock biomass (Fig 3A & B). Yet, if fishing rate remains near its previous 10-year average, the population is predicted to move 50-100 km northward during the 21st century and 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 New York in 10%-30% of the years from 2010 to 2100. In the past 5-7 years 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 maximum sustainable yield (MSY) and to the fishing mortality rate (F_{MSY}) which, if applied constantly, would result in MSY (ASMFC 2005). Under all three climate scenarios, F_{MSY} and MSY increase compared to estimates based on average minimum winter air temperatures over the past 30 years (Fig. 4). The yield curve flattens at higher temperatures, so comparing F_{MSY} is somewhat arbitrary (a range of F's result in similar yields), but forecasted MSY's are 28%, 60%, and 106% higher under the commit, B1, and A1B climate scenarios compared to the estimated MSY based on observed minimum winter temperatures over the past 30 years (Table 3).

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 and 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 the species and we forecast that climate change will have positive effects on the species in this region (increased abundance and range). For species with populations at the southern end of the distribution, similar modeling has forecast opposite results. For example, in this same ecosystem, Atlantic cod is predicted to shift northwards 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. 2007). 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. 2007). 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 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 weight-at-age and maturity-at-age schedules could be linked to temperature (Brander 1995, Godø 2003). The model is a single-species model, and certainly species interactions will affect the population and could be included in future modeling efforts (Overholtz and Link 2007). Also, we are dealing only with the northern stock of Atlantic croaker along the east coast of the United States (ASMFC 2005); climate effects on the population along the southeast U.S. coast and in the Gulf of Mexico are likely, but not considered. Although our model does not include all the potential complexities, it is based on a mechanistic recruitment hypothesis that is supported by both laboratory (Lankford and Targett 2001a, b) and field work (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 include climate change in a forecasting model for use in fisheries management.

Our forecasts are long-term, average projections for the mid-Atlantic croaker population. It is important to realize that there is substantial interannual variability in historical and forecasted temperatures, as well as in Atlantic croaker recruitment. Our longer-term forecasts could be complemented by shorter-term forecasts. 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. However, as our work shows, these forecasts need to include both the effect of fishing and the effect on climate on population dynamics.

This work demonstrates that quantitative coupled climate-population models for fishery species are tractable 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 indexed by air temperature. To develop climate-population models in these instances, climate models need to represent mechanistic hypotheses linking the regional oceanic 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, as well as to future assessments of the effect of climate change on regional resources, ecosystems, and economies (IPCC 2007a).

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Table 1. Age-specific parameters used in the population model: weight-at-age (W_A), proportion mature-at-age (M_A), and proportional availability to fishing-at-age (s_A). These values were taken from the most recent stock assessment (ASMFC 2005).

Parameter	Age										
	0	1	2	3	4	5	6	7	8	9	10+
W_A (kg)	0.05	0.12	0.22	0.32	0.43	0.52	0.61	0.68	0.74	0.79	0.83
M_A (proportion)	0	0.9	1	1	1	1	1	1	1	1	1
s_A (proportion)	0.06	0.50	0.67	0.83	0.97	0.97	0.97	0.97	0.97	0.97	0.97
N_{1900}	3.4e8	7.5e7	6.8e7	1.3e8	9.2e7	2.7e7	5.6e6	1.7e7	1.1e7	8.2e6	1.7e7

Table 2. Time specific fishing mortality rates used in the coupled climate-population model. Values from 1900-2005 were used in the hindcasting portion of the model and values from 2006 to 2100 were used in the forecasting portion of the model.

Years	F
1900-1934	0.2
1935-1944	0.3
1945-1954	1.3
1955-1964	0.8
1965-1982	0.6
1983-2005	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 (μ=0, σ=0.02)

Table 3. Maximum sustainable yield (*MSY*) and fishing rate at maximum sustainable yield (F_{MSY}) based on three CO_2 emission scenarios simulated with the GFDL CSM 2.1. Also, provided are the values based on the most recent stock assessment; the values presented here are slightly different than those presented in the assessment for Atlantic croaker (37) because the model form used here (an environmentally-explicit Ricker stock-recruitment function) is different than that used in the stock assessment (a standard Beverton-Holt function).

Scenario	F_{MSY}	Yield (*MSY*) (kg)
A1B	0.92	3.77×10^7
B1	0.73	3.04×10^7
Commit	0.60	2.43×10^7
Observed	0.48	1.87×10^7

Figure legends

Fig. 1. Relationship between Atlantic croaker recruitment and minimum winter air temperature 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 and recruitment of Atlantic croaker ($r=0.68$, $p<0.001$). B) Environmental stock-recruitment relationship for Atlantic croaker ($r^2= 0.61$, $p<0.001$). Estimates of recruitment are shown for three fixed temperatures. C and 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 (29). Modeled values are shown as the mean ± standard deviation of 100 runs of the coupled climate-population model.

Fig. 2. Observations and global climate model projections of minimum winter air temperature in Virginia, U.S. from 1900 to 2100. Results from three CO_2 emission scenarios from the GFDL CM2.1 model are shown. Long-term trends in temperature are represented by a 40 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.

Fig. 3. Forecasts of the effects of climate change on Atlantic croaker abundance and distribution along the mid-Atlantic coast of the United States. A) Forecast mean spawning stock biomass (2010 to 2100) for three climate scenarios (commit, B1, and

A1B) and a range of fishing mortality rates. Spawning stock biomasses are significantly different among climate scenarios at most levels of fishing mortality rate. B) Contours of $\frac{\partial S}{\partial T} \Big/ \frac{\partial S}{\partial F}$, which is a measure of the relative effect of climate compared to fishing. The average minimum winter air temperature from 2010 to 2100 for climate model scenario is shown by the colored triangles on the left of panel B. C) Forecasts of mean population location, D) northern extent of the range (mean + 2 standard deviations), and E) percent of years when northern extent of the population is north of the New York apex (distance 600 km). Inset shows location 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 grey contours in C, D and E. Arrows along the x-axis indicate the level of current fishing mortality rate. The average minimum winter air temperature from 2010 to 2100 for climate model scenario is shown by the colored triangles on the left of panel E.

Fig. 4. Fishery yield as a function of fishing mortality rate based on the temperature-dependent stock recruitment model (see Fig 1B) and three climate scenarios (commit, B1, and A1B). Yield curves are presented as lines; maximum sustainable yields (MSY) and fishing rates at maximum sustainable yields (FMSY) are indicated by triangles. Actual values of MSY and F_{MSY} are presented in Table A5 in the online Appendix.

Figure 1

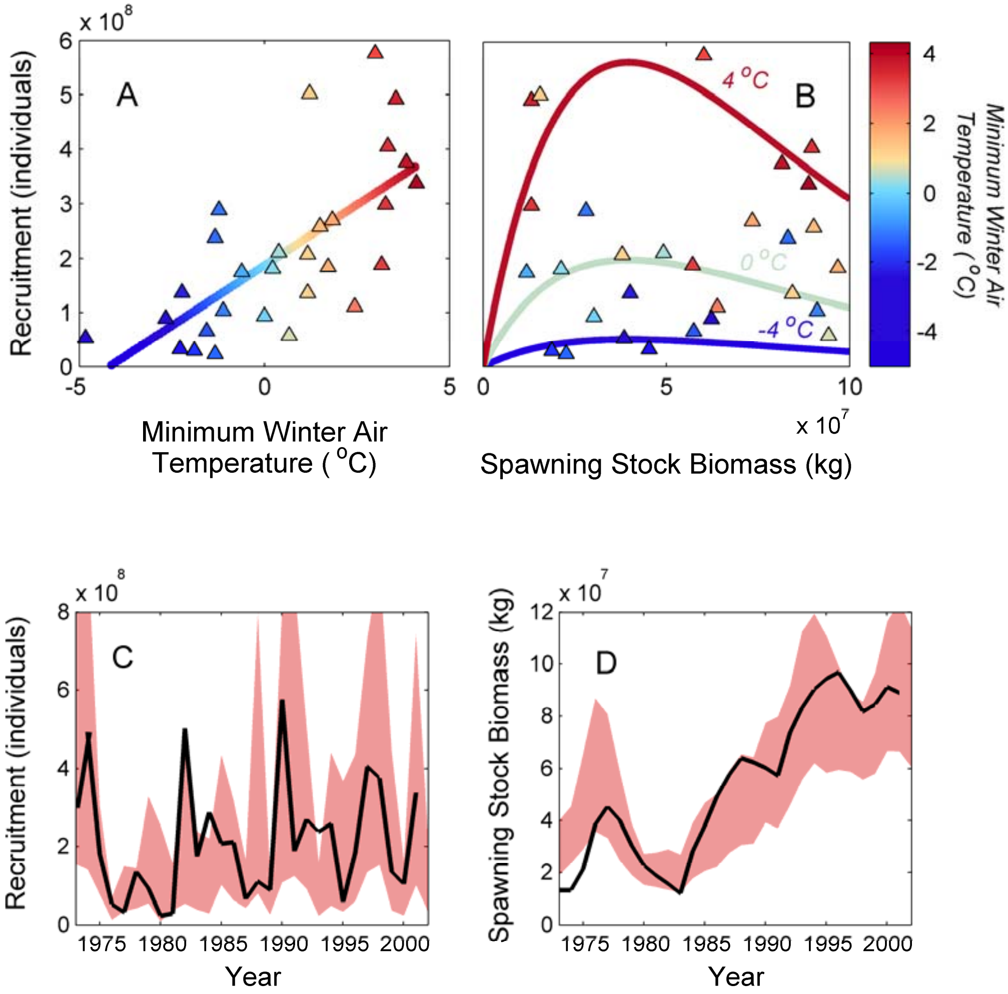

x 10^8
Recruitment (individuals)
A
Minimum Winter Air Temperature (°C)
-5
0
5
B
4 °C
0 °C
-4 °C
x 10^7
Spawning Stock Biomass (kg)
Minimum Winter Air Temperature (°C)
4
2
0
-2
-4
C
x 10^8
Recruitment (individuals)
Year
1975 1980 1985 1990 1995 2000
D
x 10^7
Spawning Stock Biomass (kg)
Year
1975 1980 1985 1990 1995 2000

Figure 2

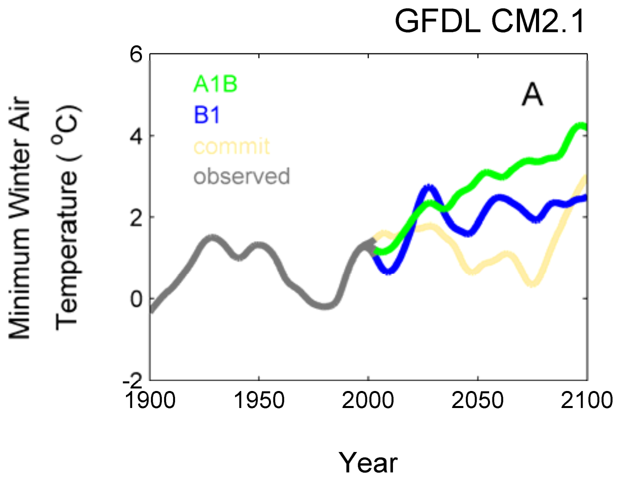

GFDL CM2.1
A
A1B
B1
commit
observed
Minimum Winter Air Temperature (°C)
6
4
2
0
-2
1900
1950
2000
2050
2100
Year

Figure 3

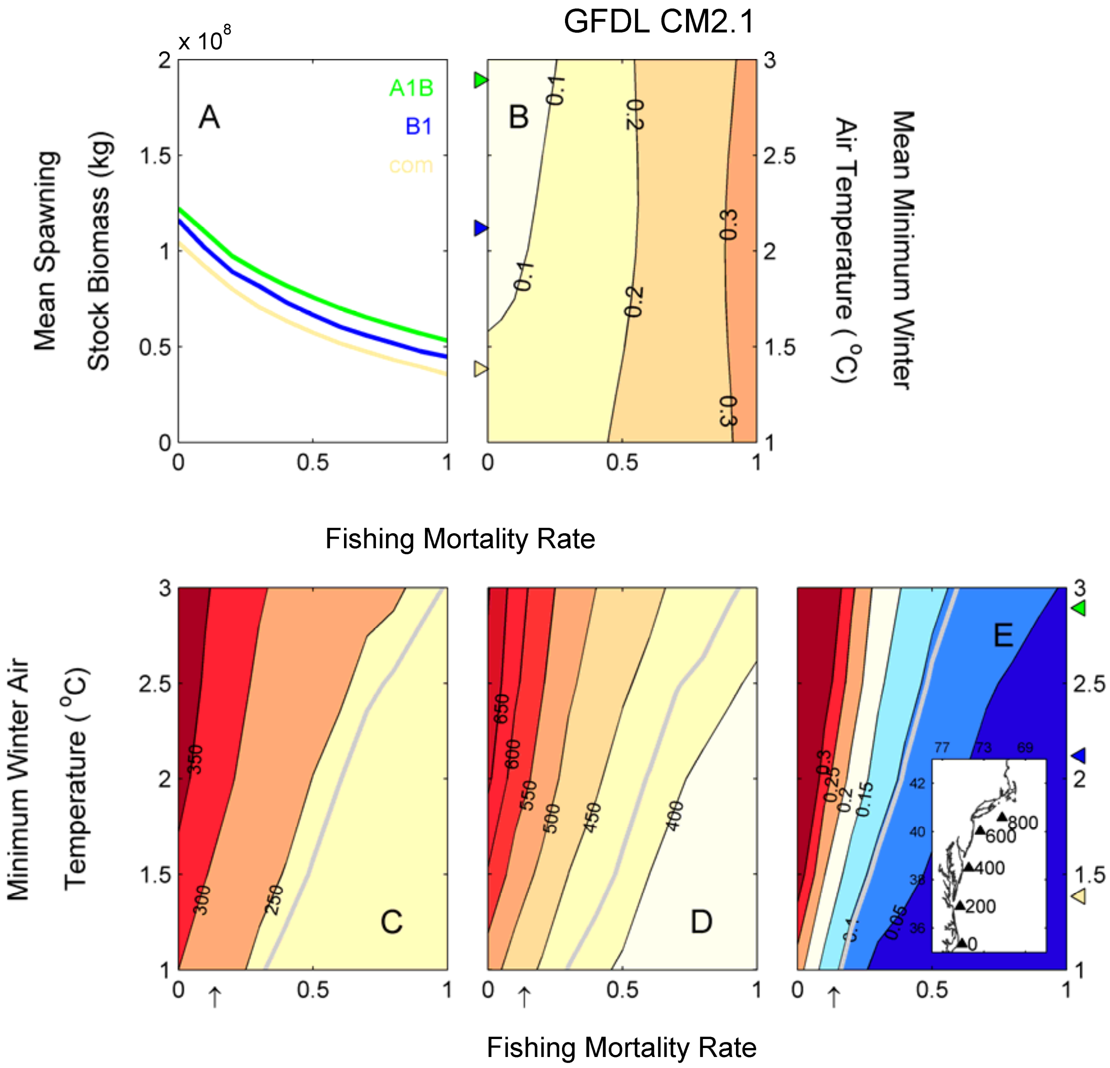
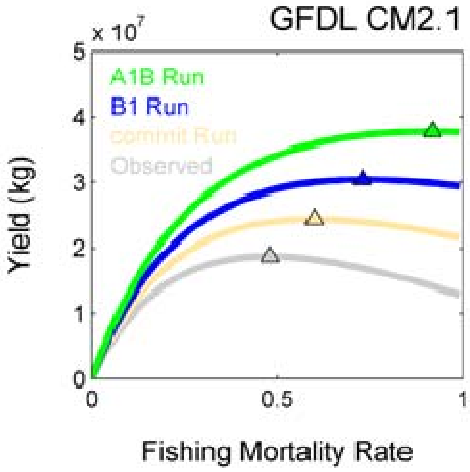

GFDL CM2.1
x 10^8
A
A1B
B1
com
Mean Spawning Stock Biomass (kg)
B
0.1
0.2
0.3
Mean Minimum Winter Air Temperature (°C)
Fishing Mortality Rate
C
350
300
250
D
650
600
550
500
450
400
E
0.3
0.25
0.2
0.15
0.1
0.05
77
73
69
42
40
38
36
800
600
400
200
0
Minimum Winter Air Temperature (°C)
Fishing Mortality Rate
0
0.5
1
1.5
2
2.5
3

Figure 4


GFDL CM2.1
x 10^7
A1B Run
B1 Run
commit Run
Observed
Yield (kg)
0
1
2
3
4
5
0
0.5
1
Fishing Mortality Rate