

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

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1 **Abstract**

2 Marine fisheries management strives to maintain sustainable populations while allowing
3 exploitation. However, well-intentioned management plans may not meet this balance as
4 most do not include the effect of climate change. Ocean temperatures are expected to
5 increase through the 21st century, which will have far-reaching and complex impacts on
6 marine fisheries. To begin to quantify these impacts for one coastal fishery along the east
7 coast of the United States, we develop a coupled climate-population model for Atlantic
8 croaker (*Micropogonias undulatus*). The model is based on a mechanistic hypothesis:
9 recruitment is determined by temperature-driven, overwinter mortality of juveniles in
10 their estuarine habitats. Temperature forecasts were obtained from 14 General Circulation
11 Models simulating three CO₂ emission scenarios. An ensemble-based approach was used
12 in which a multimodel average was calculated for a given CO₂ emission scenario to
13 forecast the response of the population. The coupled model indicates that both
14 exploitation and climate change significantly affect abundance and distribution of
15 Atlantic croaker. At current levels of fishing, the average (2010-2100) spawning biomass
16 of the population is forecast to increase by 60-100%. Similarly, the center of the
17 population is forecast to shift 50-100 km northwards. A yield analysis, which is used to
18 calculate benchmarks for fishery management, indicates that the maximum sustainable
19 yield will increase by 30-100%. Our results demonstrate that climate effects on fisheries
20 must be identified, understood, and incorporated into the scientific advice provided to
21 managers if optimum exploitation is to be achieved in a changing climate.

22

23 **KEYWORDS:** Climate change, fishery management, population dynamics, abundance,
24 distribution, environmental effects, Atlantic croaker

25

26 **Introduction**

27 Overexploitation results in dramatic declines in marine population abundance and
28 affects overall marine ecosystem structure. Fishing is often the dominant source of post-
29 juvenile mortality for exploited species, causing direct reductions in population
30 abundance (Myers et al. 1997, Christensen et al. 2003). Most fishing practices truncate
31 the age and size distribution through increased mortality and size-selectivity, which
32 potentially reduces reproductive potential of the population because larger females may
33 produce more and higher quality offspring (O'Farrell and Botsford 2006, Scott et al.
34 2006). Fishing also impacts marine ecosystems that support fisheries both directly,
35 through the effects of fishing gear on habitats (Barnes and Thomas 2005, Reed et al.
36 2007), and indirectly, with the alteration of trophic pathways through the selective
37 removal of species as targeted catch or bycatch (Jackson et al. 2001, Frank et al. 2005).
38 Fisheries management strives to balance the exploitation of a select group of species
39 against the sustainability of marine species and marine ecosystems, as well as the human
40 communities and economic activity that fisheries and marine ecosystem support ((NRC)
41 1999, Hilborn et al. 2003).

42 Environmental variability and climate change also impact marine fisheries (Koster et
43 al. 2003, Drinkwater et al. in press). Recruitment - the process by which young fish join
44 the adult or exploited population - is highly variable in most marine fish populations,

45 largely as a result of environmental variability (Rothschild 1986). Growth and maturity
46 rates are also affected by environmental variability including abiotic (e.g., temperature)
47 and biotic (e.g., availability of food) factors (Brander 1995, Godø 2003). Yet, most
48 fisheries stock assessments, which form the scientific basis for fisheries management, do
49 not include the effect of the environment on populations; environmental effects are
50 assumed to be the same in the future as in the past and thus, are already reflected in the
51 biological characteristics of the population (Richards and Maguire 1998, Hilborn and
52 Walters 2004).

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

64 Incorporating environmental effects in models for exploited fishery populations is not
65 new (Hilborn and Walters 2004). Although correlative relationships are often used,
66 numerous studies have indicated that to use environmentally-explicit population models

67 in forecasting (predicting the status of the population in the future based on
68 environmental predictions), requires a mechanistic understanding between environmental
69 forcing and population dynamics (Myers 1998, Krebs and Berteaux 2006, Hollowed et al.
70 2009). In the context of climate change, environment-population models have been
71 developed for fisheries; for example Atlantic cod abundance in the North Sea and the
72 Gulf of Maine in the future is likely to be lower than currently assessed, raising the
73 possibility of overexploitation even under management strategies designed to prevent
74 overfishing unless target levels of exploitation are adjusted accordingly (Clark et al.
75 2003, Cook and Heath 2005, Fogarty et al. 2008). These studies demonstrate that climate
76 effects on fisheries have important consequences for the long-term sustainability of
77 exploited populations.

78 We examine the effect of climate change on Atlantic croaker (*Micropogonias*
79 *undulatus*, Teleostei: Perciformes: Sciaenidae) based on a mechanistic recruitment
80 hypothesis. Atlantic croaker is a coastal marine fish inhabiting the east coast of the
81 United States (Murdy et al. 1997) that supports a fishery of approximately 9,000 metric
82 tons with a value of approximately 8 million dollars (National Marine Fisheries Service
83 2008). Atlantic croaker spawn pelagic eggs (~ 1 mm in diameter) in the coastal ocean
84 during late-summer, fall, and winter. Late-larvae enter estuaries (e.g., Delaware Bay,
85 Chesapeake Bay, Pamlico Sound) after 30-60 days in the plankton (Warlen 1982), and
86 juveniles spend their first winter in estuarine nursery habitats (Able and Fahay 1998).
87 Juvenile survival through the winter is determined by estuarine water temperatures; cold
88 water leads to low survival, which in turn decreases recruitment to the population. This

89 mechanistic recruitment hypothesis is supported by laboratory results (Lankford and
90 Targett 2001a, b) and field observations (Norcross and Austin 1981, Hare and Able
91 2007).

92 We incorporate this hypothesis into a population model with recruitment as a function
93 of spawning stock biomass and minimum winter temperature. We then couple this
94 population model with forecasts of minimum winter temperature from 14 General
95 Circulation Models (GCMs) based on three CO₂ emission scenarios. We model the
96 abundance, distribution and yield of the population under different climate change
97 scenarios and different fishing rates. We find that both climate and fishing affect the
98 dynamics of the population and conclude that climate change will have major
99 consequences for the Atlantic croaker population of the east coast of the United States in
100 the coming decades.

101

102 **Materials and Methods**

103 *Climate Models* - The Fourth Assessment Report of the Intergovernmental Panel on
104 Climate Change (IPCC) (IPCC 2007b) included simulations from 23 different GCMs run
105 with standardized CO₂ emission scenarios. Here we use 14 of these models (Table 1), and
106 three emission scenarios: commitment scenario in which atmospheric CO₂ is fixed at 350
107 ppm through the 21st century, the B1 scenario in which CO₂ increases to 550 ppm by the
108 end of the 21st century, and the A1B scenario in which CO₂ increases to 720 ppm by the
109 end of the 21st century (IPCC 2007b). The 14 GCM's were chosen because the results
110 are publically available for the three climate scenarios (commit, B1, and A1B) and for a

111 retrospective analysis of the 20th century (IPCC Data Distribution Centre,
112 http://www.mad.zmaw.de/IPCC_DDC/html/SRES_AR4/index.html). Also, the models
113 and scenarios included had simulations through 2100. Some of the models have more
114 than one run for one or more of the climate scenarios; only one run was included for each
115 model and scenario to ensure that the models were treated similarly. A comparison of
116 retrospective 20th century analysis from each GCM and observed minimum winter air
117 temperatures (1895-2007) was used to bias correct the model results; mean of model
118 outputs were compared to observations and the difference was added to minimum winter
119 air temperatures forecasted by the model (comparisons are provided in the Appendix,
120 Section 1).

121 Air temperature, which is forecast in most GCMs, is a good proxy for estuarine water
122 temperatures owing to the efficient ocean-atmosphere heat exchange in estuarine systems
123 (Roelofs and Bumpus 1953, Hare and Able 2007). Winter air temperature is also strongly
124 coherent along the U.S. east coast (Joyce 2002) and one location can be used as a proxy
125 for a larger area (Appendix, Section 1). Thus, minimum winter air temperature in the
126 Chesapeake Bay region is used as the climate input into the coupled climate-population
127 model. The Chesapeake Bay region was chosen because this estuary is a major Atlantic
128 croaker overwintering nursery (Murdy et al. 1997, Able and Fahay 1998).

129

130 *Population Model* – A finite time step model (Fogarty 1998, ASMFC 2005) was
131 developed for the population of Atlantic croaker along the mid-Atlantic coast of the
132 United States. Spawning stock biomass (S) in a given year was calculated as the sum of

133 the number of individuals (N) at each age (A) in that year (y) multiplied by a constant
 134 weight-at-age (W_A), a constant percent mature at age (M_A), and a constant sex ratio
 135 ($SR=0.5$).

$$136 \quad S_y = \sum_A N_{Ay} \cdot W_A \cdot M_A \cdot SR \quad (1)$$

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

139 The mechanistic hypothesis that recruitment is determined by winter water
 140 temperatures affecting mortality during the juvenile stages was incorporated into the
 141 model using an environmentally explicit stock recruitment relationship. In the model,
 142 numbers-at-age 1 in year y (N_{1y}) equaled recruitment in year y (R_y). Recruitment in year y
 143 was calculated based on spawning stock biomass in year $y-1$ (S_{y-1}) with the addition of the
 144 term for minimum winter temperature during year $y-1$ (Dec) and year y (Jan, Feb, and
 145 Mar) (denoted T_y).

$$146 \quad N_{1y} = R_y = aS_{y-1}e^{(-b \cdot S_{y-1} + cT_y + \varepsilon)} \quad (2)$$

147 This form of the stock-recruitment relationship was used because it provided the best fit
 148 to observed data (Appendix, Section 2). The climate effects on the population entered the
 149 model through the temperature term (T). Error in the stock recruitment relationship (ε)
 150 was included formally in the model as a normally distributed random variable
 151 parameterized from the fit of the model to data.

152 Number-at-age in a given year (N_{Ay}) was calculated from number at the prior age in
 153 the prior year ($N_{A-1 y-1}$) discounted by mortality, which was spilt into two components:

154 fishing mortality (F) and natural mortality (M). Fishing mortality is an instantaneous rate
155 used to calculate how many fish are removed from a population through fishing over a
156 period of time. Natural mortality is similar but used to calculate how many fish are
157 removed from a population through natural causes (e.g., predation, disease) over a period
158 of time. Fishing mortality was multiplied by an age-dependent selectivity coefficient (s_A ,
159 Table 2), because younger ages are less susceptible to capture in the fishery compared to
160 older individuals.

161
$$N_{Ay} = N_{(A-1)(y-1)} e^{-(Fs_{A-1}+M)} \quad (3)$$

162 The model was implemented for 1900 to 2100 using observed (1900-2007) and
163 simulated (2008-2100) minimum winter air temperatures. Natural mortality (M) was
164 assumed to be constant with a normally distributed random component ($\mu=0.3$, $\sigma=0.05$);
165 this value was taken from the recent stock assessment (ASMFC 2005). For model
166 hindcasts, historical fishing mortality rates (F) were set to levels consistent with the
167 history of the fishery (Table 3). For model forecasts, rates of fishing (F) ranged from 0 to
168 1 with a random component ($\mu=0$, $\sigma=0.02$). For each climate scenario and GCM, 100
169 population simulations were calculated to include the variability associated with
170 stochasticity in natural mortality (M), fishing mortality (F), and the unexplained
171 variability in recruitment (ε).

172 The outputs from the coupled model were averaged over time (2010-2100),
173 because GCMs do not produce annual predictions; i.e., due to random climate variability,
174 a given year in the model is not expected to match that in nature. The 14 GCMs were
175 treated as a multimodel ensemble (Reichler and Kim 2008) – the results of the different

176 GCMs were combined to make inferences about the effect of climate change on the
177 Atlantic croaker population. Two approaches were used to evaluate the output of the
178 coupled model: i) the distribution of model results were compared to past estimates of
179 spawning stock biomass (1972-2004) and ii) a multimodel mean spawning stock biomass
180 was calculated for each climate scenario across all 14 GCMs. Our results represent the
181 mean response of the Atlantic croaker population to several climate change scenarios
182 over the 21st century for an ensemble of GCMs.

183

184 *Distribution Model* – The mid-Atlantic croaker stock makes annual south-to north
185 migrations from wintering grounds off the Carolinas to summering grounds from North
186 Carolina to New Jersey (Murdy et al. 1997). Atlantic croaker also exhibit onshore-
187 offshore migrations from nearshore and estuarine areas in summer to coastal and shelf
188 areas in fall (Murdy et al. 1997). We used a multiple-regression approach to model the
189 mean distance and northern extent of the population as a function of spawning stock
190 biomass and the previous year's minimum winter temperature. Mean distance and
191 northern extent estimates were calculated from data collected by the autumn trawl survey
192 of the National Marine Fisheries Service (Azarovitz 1981). This survey is based on a
193 random stratified design, with multiple randomly located trawl stations in each strata,
194 which are defined by along-shelf regions and bathymetric zones (Azarovitz 1981).

195 Since the northeast U.S. shelf does not run simply north-south, a curvilinear grid
196 of distance from Cape Hatteras, North Carolina was developed; the grid approximately
197 followed the 10 m isobath. This grid was then used to convert each strata average

198 location (latitude and longitude) to a strata average along-shelf distance from Cape
199 Hatteras. Using average catch in each strata and average distance to each strata, we
200 calculated a weighted-mean distance for Atlantic croaker in each year. We also calculated
201 weighted standard deviation of distance. Based on the idea that range expands at higher
202 population sizes (MacCall 1990) and the suggestion that summer distribution may be
203 influenced by temperatures during the previous winter (Murdy et al. 1997), we developed
204 an empirical model for mean location ($dist_{\mu}$) and its standard deviation ($dist_{\sigma}$), based on
205 spawning stock biomass (S) and temperature (T).

$$206 \quad dist_{\mu Y} = a_u + b_u S_Y + c_u T_Y + d_{\mu} S_Y^2 + e_u T_Y^2 \quad (4)$$

$$207 \quad dist_{\sigma Y} = a_{\sigma} + b_{\sigma} S_Y + c_{\sigma} T_Y + d_{\sigma} S_Y^2 + e_{\sigma} T_Y^2 \quad (5)$$

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

216 For distribution forecasts, spawning stock biomass estimates from the coupled
217 climate-population model were combined with minimum winter temperature estimates
218 from the GCM scenarios. The outputs from the distribution model were averaged over the
219 period of 2010-2100, similar to the results of the population model. We used the mean

220 and standard deviation models to forecast the mean and northern extent of the population;
221 the latter was defined as the mean plus 2 standard deviations. In addition to mean center
222 of the distribution and mean northern extent, the frequency of years with the northern
223 extent past the Hudson Canyon was quantified. Historically, Hudson Canyon is near the
224 absolute northern limit of the population and is an important geographic feature on the
225 northeast U.S. continental shelf separating the Mid-Atlantic region from the Southern
226 New England region (Sherman 1980).

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

236

237 *Yield Analysis* - We estimated the fishing rate threshold and yield target under current
238 conditions and under the three CO₂ emission scenarios based on the temperature-
239 dependent recruitment model. The purpose was to calculate management benchmarks for
240 the population under the different climate change scenarios. The environmentally explicit
241 stock-recruitment relationship (equation 2), can be linearized:

242
$$\log_e \left[\frac{R_y}{S_{y-1}} \right] = \log_e a - bS_{y-1} + cT_y \quad (6)$$

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

244
$$S_{y-1} = \frac{I}{b} \left\{ \log_e \left[a \left(\frac{S_{y-1}}{R_y} \right) \right] + cT_y \right\} \quad (7)$$

245 Note that the expression inside the brackets includes spawning biomass-per-recruit (S/R).

246 Given estimates of the parameters of the recruitment models and standard yield and
 247 spawning biomass-per-recruit analyses (Lawson and Hilborn 1985, Quinn and Desiro
 248 1999), estimates of S/R are substituted for different levels of fishing mortality [here
 249 designated as $(S/R)_F$] to determine the total spawning biomass for each fishing mortality
 250 rate. Once the total spawning biomass corresponding to a particular level of fishing
 251 mortality (S_F) was determined, the corresponding recruitment was obtained by the simple
 252 identity.

253
$$R_F = \frac{S_F}{(S/R)_F} \quad (8)$$

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

257
$$Y_F = (Y/R)_F R_F \quad (9)$$

258 The fishing rate at maximum sustainable yield (F_{MSY}) is defined as the F resulting in the
 259 maximum sustainable yield ($MSY = \max(Y_F)$). These equations were applied to the

260 average S and R forecasts for each climate scenario resulting is MSY and F_{MSY} for each
261 climate scenario.

262

263 **Results**

264 *Environmentally explicit stock recruitment relationship* - Observed recruitment of
265 Atlantic croaker in the mid-Atlantic region is significantly correlated to minimum winter
266 air temperature (Fig. 1A), strongly supporting the mechanistic recruitment hypothesis.
267 Including a temperature term in the stock recruitment model provides a significantly
268 better fit compared to including spawning stock biomass alone (Appendix, Table A2) and
269 explains 61% of the variance in recruitment (Fig. 1B). Including temperature in the stock
270 recruitment relationship permitted the detection of a significant compensatory population
271 effect (e.g., a domed shaped stock recruitment function) that was masked by temperature-
272 driven variability. Simulated recruitment and spawning stock biomass largely overlapped
273 with spawning stock biomass and recruitment from the stock assessment (ASMFC 2005)
274 providing confidence that the model captures the large-scale dynamics of the population
275 (Fig. 1C and 1D).

276

277 *Minimum winter temperatures* - As the level of atmospheric CO_2 increases, GCMs
278 predict that minimum winter temperatures in the Chesapeake Bay region of the United
279 States will increase. Under the commit scenario (CO_2 constant at 350 ppm), the models
280 predict little trend in minimum winter temperatures; fluctuations are dominated by
281 natural variability within the climate system (Fig. 2). In contrast, under the B1 and A1B

282 scenarios, the models predict increasing minimum winter air temperatures with values
283 higher than observed during the 20th century.

284

285 *Population abundance* - With increasing minimum winter temperatures, the coupled
286 climate-population model predicts that Atlantic croaker abundance will increase (Fig. 3).
287 Increased temperatures result in higher recruitment, which leads to higher spawning stock
288 biomass. At current levels of fishing mortality ($F=0.11$), all GCMs and all scenarios
289 predicted higher population abundances than observed since the early 1970's. Ensemble-
290 mean increases in spawning stock biomass of 63%, 82% and 92% are projected under the
291 commit, B1, and A1B scenarios. Fishing also influences abundance; as fishing mortality
292 increases, spawning stock biomass decreases. Counteracting warming, forecast spawning
293 stock biomass decreases as fishing mortality increases, but even at higher fishing
294 mortality rates ($F=0.4$), all GCMs for the B1 and A1B scenarios predict higher population
295 abundances than observed in the past. These results are intuitive based on the structure of
296 the model and the relationship between temperature and recruitment, but unless fishing
297 mortality increases by more than fourfold, the coupled population-climate model
298 indicates that Atlantic croaker biomass will increase in the future.

299 The model also allows the effect of climate change on population dynamics to be
300 quantified relative to the effect of fishing through the comparison of the partial

301 derivatives of spawning stock biomass (S) relative to climate scenario (C) ($\frac{\partial S}{\partial C}$) and

302 fishing (F) ($\frac{\partial S}{\partial F}$) (Figure 4). As fishing mortality rate increases, $\frac{\partial S}{\partial F}$ decreases. In

303 contrast, $\frac{\partial S}{\partial C}$ remains relatively constant over the range of fishing mortality rates. As a
304 result, at lower fishing mortality rates, the effect of climate is 10-20% of the effect of
305 fishing, while at higher fishing mortality rates, the effect of climate is 20-30% of the
306 effect of fishing. In other words, an increase in atmospheric CO₂ from 350 to 550 ppm is
307 approximately equivalent to a 0.2 decrease in fishing mortality rate. This is a substantial
308 effect given that the estimated range of fishing mortality on Atlantic croaker was 0.03 to
309 0.49 from 1973-2002 (ASMFC 2005).

310

311 *Population distribution* - The empirical distribution model predicts that with increasing
312 minimum winter air temperatures, the range of Atlantic croaker will expand northward.
313 Fishing also has a strong effect on distribution, because fishing mortality affects
314 spawning stock biomass (Fig 5). At zero fishing mortality, all climate models and
315 scenarios forecast a northward shift in the population of 50-200 km; the shift is greater at
316 higher levels of atmospheric CO₂. Likewise, the northern extent of the distribution is
317 forecast to shift 100-400 km northwards and the frequency north of Hudson Canyon
318 increases 10-40%, depending on the GCM and CO₂ emission scenario. As fishing
319 mortality increases to 0.1 (the current level) and 0.4, the range expansions are predicted
320 to be less. At current levels of fishing (0.1), however, all B1 and A1B scenarios and most
321 commit scenarios forecast a northward expansion of range. At relatively high fishing
322 mortality rates (0.4), most models predict no change in mean distribution and frequency
323 north of Hudson Canyon, and only a modest increase in the northern extent of ~ 50 km.

324 The ensemble means exhibit the same patterns as described above: with increased
325 atmospheric CO₂ and resulting warming, the Atlantic croaker population will expand
326 northward if fishing remains at recent levels (Figure 6). The population is predicted to
327 move 50-100 km northward during the 21st century if fishing remains near 0.1; the
328 northern limit of the population is predicted to shift 75-175 km northward. Further,
329 interannual variability is predicted to extend the northern limit of the population past
330 Hudson Canyon in 10%-30% of the years from 2010 to 2100. Over the past decade,
331 Atlantic croaker has become a regular fishery species in Delaware Bay and coastal New
332 Jersey, and our results indicate that this trend will continue and that Atlantic croaker will
333 be observed more frequently in waters of southern New England in the coming decades.

334

335 *Population Yield* - A yield analysis based on the coupled climate-population model
336 estimates that management benchmarks for Atlantic croaker in the mid-Atlantic region
337 will change dramatically with increasing minimum winter air temperatures. Fishery
338 benchmarks are biological reference points based on exploitation characteristics of the
339 population that are used for guidance in developing fishery management strategies
340 (Restrepo et al. 1998). For Atlantic croaker, thresholds and targets for fishing rate and
341 spawning stock biomass have been defined relative to an estimated maximum sustainable
342 yield (*MSY*) and to the fishing mortality rate (F_{MSY}), which, if applied constantly, would
343 result in *MSY* (ASMFC 2005). Based on ensemble averages across all GCM scenarios,
344 F_{MSY} and *MSY* increase under all three climate scenarios compared to estimates based on
345 average minimum winter air temperatures over the past 30 years (Fig. 7). The yield curve

346 flattens at higher fishing mortality rates, so comparing F_{MSY} is somewhat arbitrary (a
347 range of F 's result in similar yields), but forecasted MSY 's are 35%, 73%, and 96%
348 higher under the commit, B1, and A1B climate scenarios compared to the estimated MSY
349 based on observed minimum winter temperatures over the past 30 years (Table 4).

350

351 **Discussion**

352 We conclude that both fishing and climate change impact the abundance and
353 distribution of Atlantic croaker along the mid-Atlantic coast of the United States. Climate
354 change also affects benchmarks used in fisheries management; MSY and F_{MSY} increase
355 with increasing temperatures. Thus, benchmarks for the mid-Atlantic stock of Atlantic
356 croaker set without consideration of climate change would be precautionary (Restrepo et
357 al. 1998). The mid-Atlantic region represents the northern limit of Atlantic croaker and
358 we forecast that projected temperature increases will have positive effects on the species
359 in this region (increased abundance and range) not considering other effects of climate
360 change and ocean acidification (Doney et al. 2009, Drinkwater et al. in press). For species
361 with populations at the southern end of the distribution, similar modeling has forecast
362 opposite results. For example, Atlantic cod is predicted to shift northwards becoming
363 expatriated from the southern New England shelf. Further, the productivity of the cod
364 fishery in the Gulf of Maine is predicted to decrease (Fogarty et al. 2008). In the instance
365 of Atlantic cod, benchmarks used in management may be set too high and this may lead
366 unknowingly to unsustainable management practices even under stringent rebuilding
367 plans (Fogarty et al. 2008). This contrast illustrates that in any region, some species will

368 be positively affected by climate change, while others will be negatively affected.
369 Further, climate change will affect the benchmarks used in fisheries management.
370 Understanding and quantifying the effect of climate change on populations in
371 combination with the effect of exploitation is a major challenge to rebuilding and
372 maintaining sustainable fisheries in the coming decades.

373 The coupled climate-population model developed here does not include all the
374 potential climatic effects on Atlantic croaker. The population model has a number of
375 parameters, all of which are potentially affected by warming temperatures: recruitment
376 (included here), weight-at-age, maturity-at-age, natural mortality, fishing mortality, and
377 catchability. The weight-at-age and maturity-at-age schedules could be linked to
378 temperature (Brander 1995, Godø 2003). Natural mortality is included as a constant, but
379 climate change may result in temporally variable predation pressure (Overholtz and Link
380 2007). Fishing mortality also may vary as fishing communities adapt to climate change
381 (e.g., (Hamilton and Haedrich 1999, Berkes and Jolly 2001, McGoodwin 2007) and
382 catchability may change as the population shifts northward, where trawl fisheries become
383 more prevalent (Stevenson et al. 2004).

384 In addition to added climate effects in the population model, there are also different
385 forms of models that could be used. Keyl and Wolff (2008) reviewed environmental-
386 population models in fisheries and found six dominant types: stock-recruit analysis,
387 surplus production models, age- or size-structured models, trophic and multi-species
388 models, individual-based models, and generalized additive models. The population model
389 used here for Atlantic croaker was an age-structured model with minimum winter

390 temperature in year y and spawning stock biomass in year y influencing recruitment in
391 year $y+1$. Time lags are built into this model since spawning stock biomass is summed
392 over age-classes, the size of which are dependent on initial recruitment and subsequent
393 mortality. Time lags also could be incorporated through temperature dependent growth
394 (weight-at-age) or maturity functions. The distribution model used spawning stock
395 biomass in year y and minimum winter temperature in year $y-1$ to predict distribution in
396 year y . Similar to the population model, time lags are incorporated into the distribution
397 model through the inclusion of spawning stock biomass. Since Atlantic croaker is a
398 migratory fish, it is also possible that migrations in previous years affect the distribution
399 in the current year, resulting in additional time lags that are not considered in the current
400 effort.

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

411 It is important to note that our effort examines Atlantic croaker at the northern part of
412 its range (ASMFC 2005). The recent assessment considers two stocks of Atlantic croaker
413 along the east coast of the United States: a northern stock (considered here) and a
414 southern stock (not considered). There is evidence that abundance of the southern stock is
415 decreasing: catch has decreased in southern states and a fishery-independent abundance
416 index of the southern stock has decreased (ASMFC 2005). These findings are consistent
417 with the hypothesis that the southern stock is declining and withdrawing northwards in
418 response to climate change, but this question has not been examined in detailed and there
419 has been little research on environmental influences on the dynamics of Atlantic croaker
420 in the southern part of the range.

421 Our forecasts are on a 50-100 year scale. Fisheries management does not operate
422 on these scales and shorter-term forecasts are required. The climate modeling community
423 is focusing great effort on developing decadal scale forecasts that include both externally
424 forced changes (e.g., CO₂ emissions) and internal variability (e.g., Atlantic meridional
425 overturning circulation, El-Niño Southern Oscillation) (Smith et al. 2007, Keenlyside et
426 al. 2008). In the future, a range of climate forecasts of the status of fish populations (5-20
427 years, 20-50 years, 50-100 years) could be provided to scientists, managers, and
428 fishers(Brander in press) . However, these forecasts need to include both the effect of
429 fishing and climate on population dynamics (Planque et al. In press).

430 Quantitative coupled climate-population models for fishery species are tractable,
431 now, under certain circumstances. In the specific example, the climate-population link
432 (survival of overwintering juveniles in shallow estuarine systems) is direct and well-

433 reproduced by current climate models. Winter temperature is an important regulatory
434 factor in many fish populations (Hurst 2007) and the effort here could be easily extended
435 to some of these species. Climate-population links for many other species will be
436 complicated and involve processes that cannot be indexed by air temperature. To develop
437 climate-population models in these instances, climate models need to represent
438 mechanistic hypotheses linking the regional oceanic environment to population
439 dynamics, and ultimately include the interactions between populations and species
440 (Winder and Schindler 2004, Helmuth et al. 2006, Cury et al. 2008). The development of
441 such coupled models will contribute to the goal of providing the best scientific advice for
442 managing fisheries in a future of changing climate (Perry et al. in press), as well as to
443 future assessments of the effect of climate change on regional resources, ecosystems, and
444 economies (IPCC 2007a).

445

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457

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644

645

646 Table 1. List of General Circulation Models (GCMs) used in this study and their
 647 associated modeling centers. Three CO₂ emission scenarios from 14 GCMs were
 648 used. Data were obtained from the Model and Data Group (M&D) at the Max-
 649 Planck-Institute for Meteorology
 650 (http://www.mad.zmaw.de/IPCC_DDC/html/SRES_AR4/index.html).

651

Modeling Center	General Circulation Model
Bjerknes Centre for Climate Research, Norway	BCM2.0
Canadian Centre for Climate Modelling and Analysis, Canada	CGCM3
Centre National de Recherches Meteorologiques, France	CM3
Australia's Commonwealth Scientific and Industrial Research Organization, Australia	Mk3.0
Meteorological Institute, University of Bonn, Germany Meteorological Research Institute of KMA, 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 Centre for Atmospheric Research, USA	CCSM3
UK Met. Office, United Kingdom	HadCM3

652

653 Table 2. Age-specific parameters used in the population model: weight-at-age (W_A),
 654 proportion mature-at-age (M_A), and proportional availability to fishing-at-age (s_A). These
 655 values were taken from the most recent stock assessment (ASMFC 2005). Also included
 656 are the numbers-at-age assumed for 1900 (N_{1900}), the first year of the simulations.

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

657

658 Table 3. Time specific fishing mortality rates (F) used in the coupled climate-population
 659 model. Values from 1900-2005 were used in the hindcasting portion of the model and
 660 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 ($\mu=0, \sigma=0.02$)

661

662

663 Table 4. Ensemble average maximum sustainable yield (*MSY*) and fishing rate at
 664 maximum sustainable yield (F_{MSY}) based on three CO₂ emission scenarios simulated with
 665 14 General Circulation Models (GCMs). Also provided are the values based on the most
 666 recent stock assessment of Atlantic croaker (ASMFC 2005); the values presented here are
 667 slightly different than those presented in the assessment because the model form used
 668 here (an environmentally-explicit Ricker stock-recruitment function) is different than that
 669 used in the stock assessment (a standard Beverton-Holt function). Multimodel ensemble
 670 mean and 95% confidence intervals are provided.

671

Scenario	F_{MSY}	Yield (<i>MSY</i>) (kg)	Confidence Intervals (kg)
A1B	0.89	3.67×10^7	$3.30-4.07 \times 10^7$
B1	0.78	3.23×10^7	$2.90-3.58 \times 10^7$
Commit	0.62	2.52×10^7	$2.24-2.82 \times 10^7$
Observed	0.48	1.87×10^7	

672

673 **Figure legends**

674 Fig. 1. Relationship between Atlantic croaker recruitment and minimum winter air
675 temperature and comparison of observed recruitment and spawning stock biomass with
676 hindcasts developed from a coupled climate-population model. A) Relationship between
677 minimum winter air temperature in Virginia and recruitment of Atlantic croaker ($r=0.68$,
678 $p<0.001$). B) Environmental stock-recruitment relationship for Atlantic croaker ($r^2=$
679 0.61 , $p<0.001$). Estimates of recruitment are shown for three fixed temperatures. C and
680 D) Comparison of observed and modeled recruitment and spawning stock biomass from
681 1973 to 2003 based on the coupled climate-population model. Observed values (black
682 lines) are from the stock assessment (ASMFC 2005). Modeled values are shown as the
683 mean \pm standard deviation of 100 runs of the coupled climate-population model.

684

685 Fig. 2. Observations and General Circulation Model (GCM) projections of minimum
686 winter air temperature in Chesapeake Bay region from 1900 to 2100. Results from three
687 CO₂ emission scenarios averaged for 14 GCMs are shown. Long-term trends in
688 temperature are represented by a 30 point lowess smoother fit to the annual series; these
689 smoothed trends included a combination of observed and modeled temperatures so the
690 divergence between observations and models occurs prior to the end of the observations.
691 Lines represent the multimodel mean of the GCMs and shading represents 95%
692 confidence intervals.

693

694 Fig. 3. Forecasts of the effects of climate change on Atlantic croaker spawning stock
695 biomass for each of 14 General Circulation Models (GCMs) and three CO₂ emission
696 scenarios at three fishing mortalities (F=0, F=-0.1, and F=-0.4). Historical levels (HM) of
697 spawning stock biomass are shown (1972-2004).

698

699 Fig. 4. A) Ensemble multimodel mean spawning stock biomass (2010 to 2100) for three
700 climate scenarios (commit, B1, and A1B) and a range of fishing mortality rates. B)

701 Contours of $\frac{\partial S}{\partial C} / \frac{\partial S}{\partial F}$, which is a measure of the relative effect of climate compared to
702 fishing. Arrows along the x-axis indicate the current fishing mortality rate.

703

704 Fig. 5. Forecasts of the effect of climate change on Atlantic croaker distribution in the
705 mid-Atlantic region of the northeast U.S. continental shelf. Mean location, northern
706 extant, and frequency north of Hudson Canyon are shown based on three CO₂ emission
707 scenarios from 14 General Circulation Models (GCMs) at three fishing mortalities (F=0,
708 F=-0.1, and F=-0.4). Historical levels (HM) of distribution measures are shown (1972-
709 2004)..

710

711 Fig. 6. A) Ensemble multimodel mean population location, B) northern extent of the
712 range (mean + 2 standard deviations), and C) percent of years when northern extent of the
713 population is north of the Hudson Canyon (distance 600 km). D) Maps of various
714 distance marks along the continental shelf. The historical values (1972-2004) of mean
715 location (~240 km), northern extent (~420 km), and proportion of years with the measure

716 of northern extent exceeding 600 km (0.09) are shown as dark grey contours. Arrows
717 along the x-axis indicate the level of current fishing mortality rate.

718

719 Fig. 7. Fishery yield as a function of fishing mortality rate based on the temperature-
720 dependent stock recruitment model (see Fig 1B) and ensemble multimodel mean of three
721 climate scenarios (commit, B1, and A1B). Yield curves are presented as lines; maximum
722 sustainable yields (MSY) and fishing rates at maximum sustainable yields (FMSY) are
723 indicated by triangles.

724

Figure 1

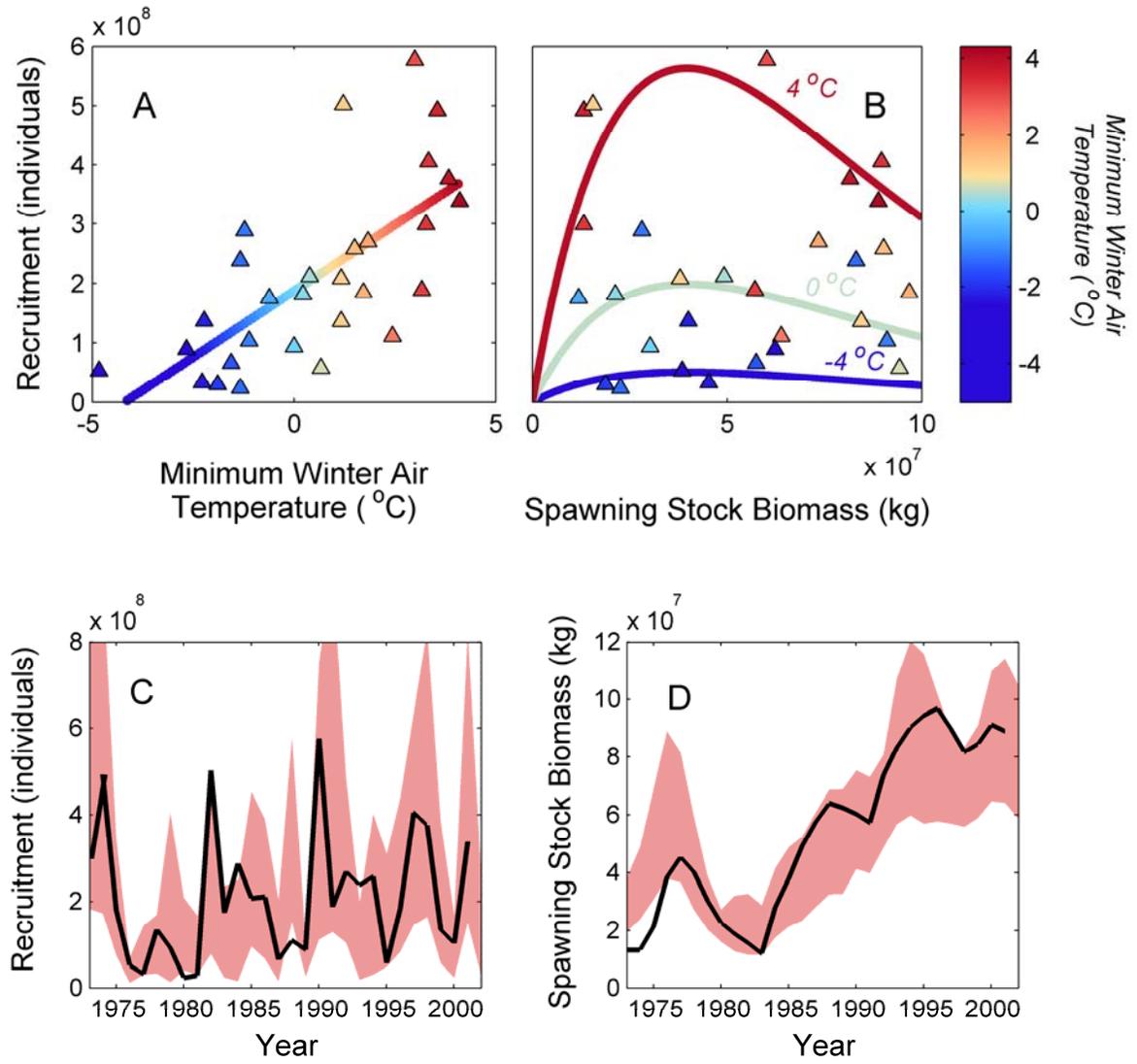


Figure 2

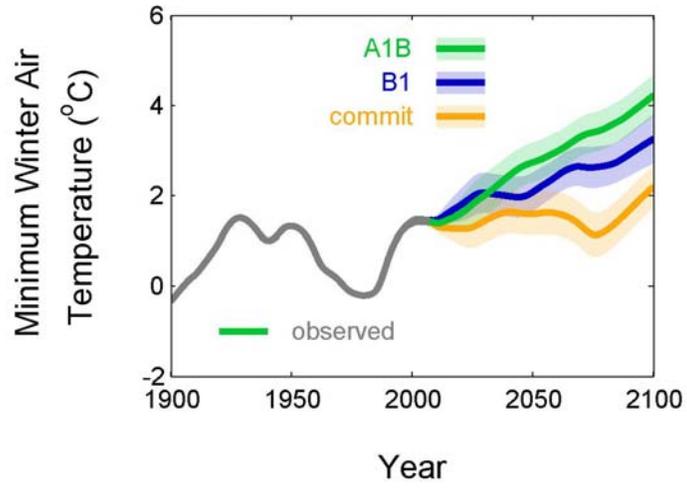


Figure 3

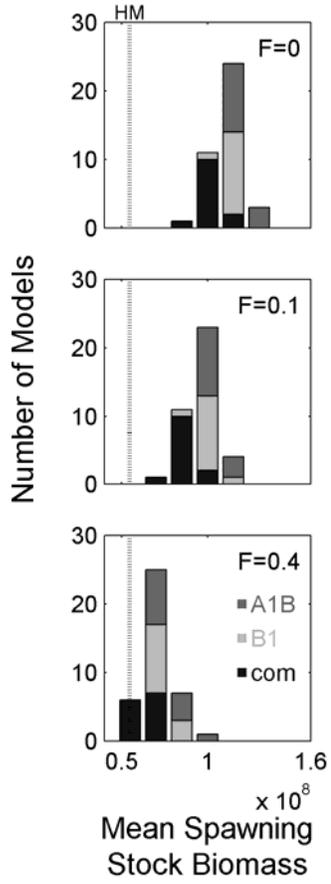


Figure 4

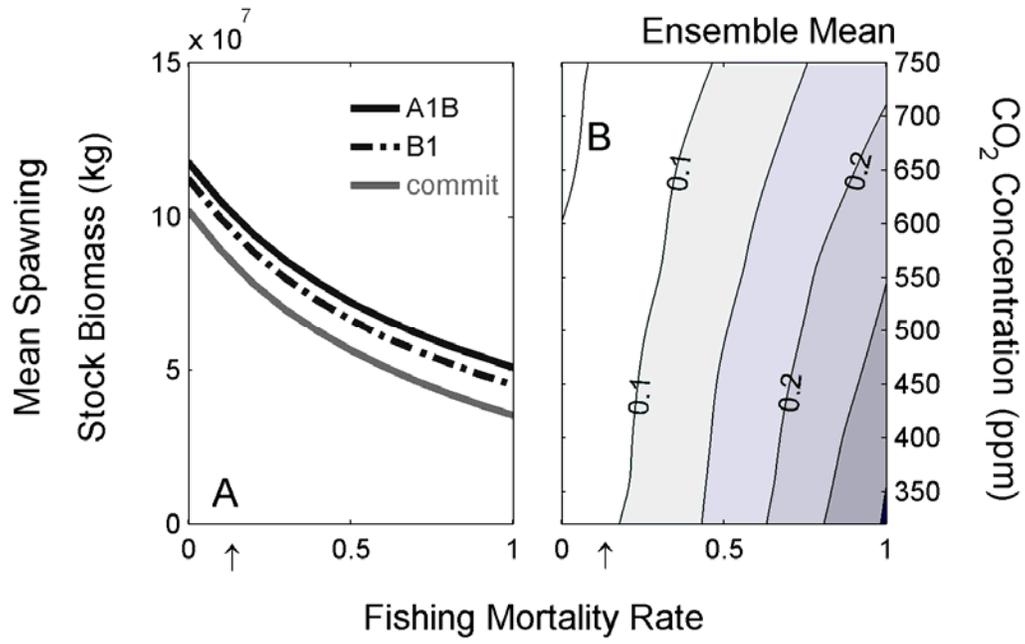


Figure 5

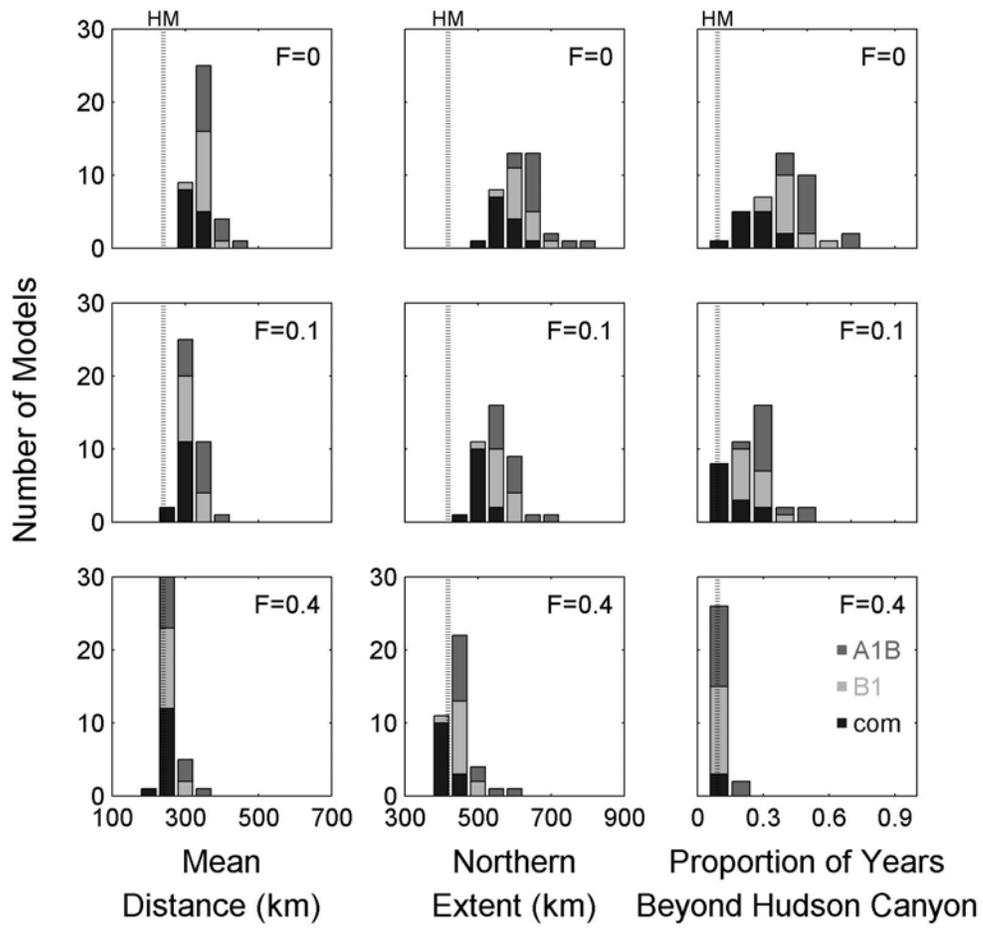


Figure 6

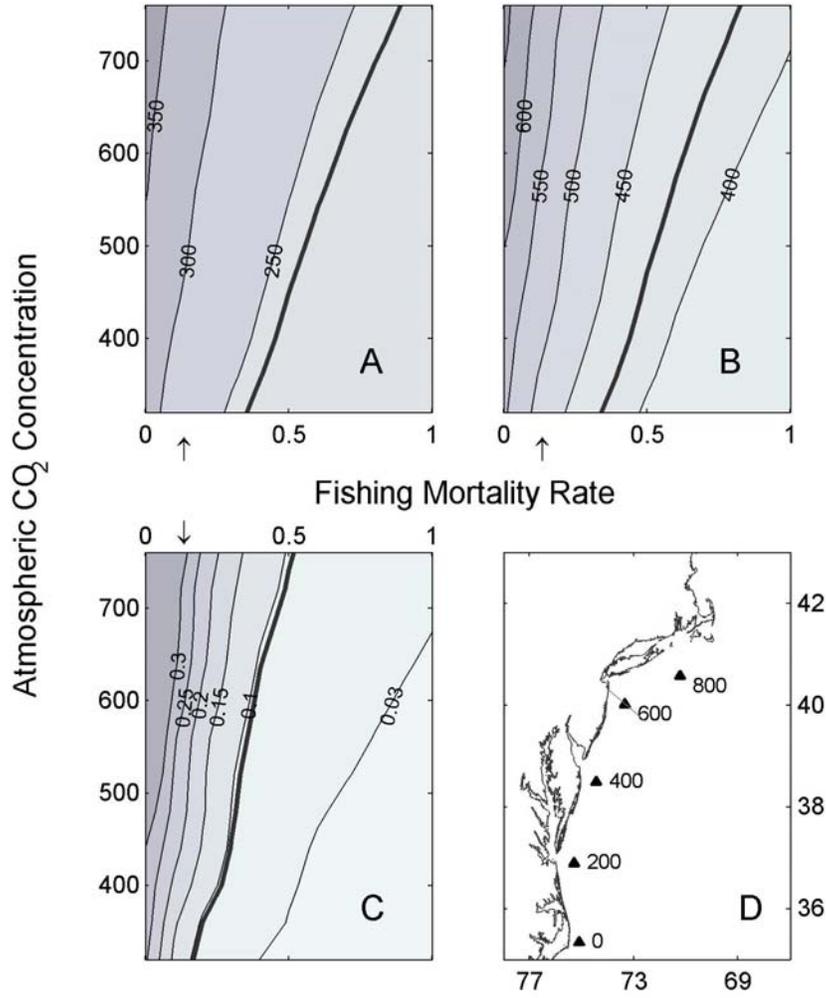
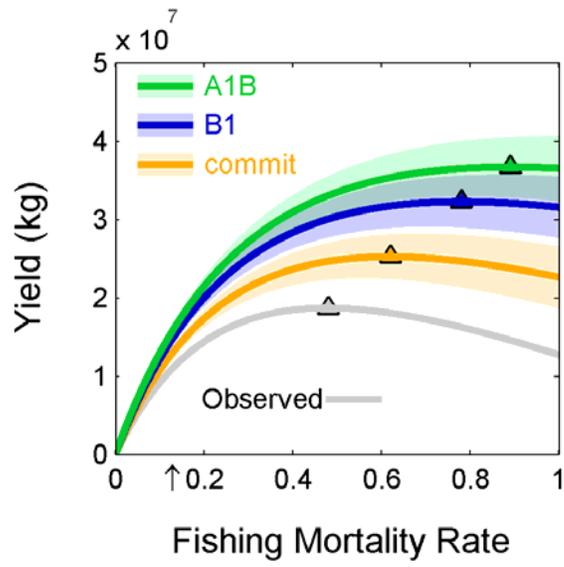


Figure 7



Online Appendix

Forecasting the Dynamics of a Coastal Fishery Species Using a Coupled Climate-Population Model

Jonathan Hare ¹, Michael Alexander ², Michael Fogarty ³, Erik Williams ⁴, James Scott ²

1. **Background on general circulation models**
2. **Choice of a stock recruitment function**
3. **Distribution model based on logistic regression**
4. **References**

1. Background on general circulation models

Annual minimum monthly winter air temperature was derived from 14 General Circulation Models (GCMs, Table A1). Also known as global climate models, GCMs depict the climate using a three dimensional grid over the globe, typically with horizontal resolutions between 250 and 600 km, 10 to 20 vertical layers in the atmosphere, and as many as 30 layers in the oceans. The resolution of these models is coarse and subgrid scale processes (e.g., turbulence in the boundary layer, thunderstorms and ocean eddies) are parameterized based on large-scale conditions, i.e., variables that are simulated on the model's coarse grid. Even at coarse resolution, the models are run on super computers as the temperature, moisture, salinity, winds, ocean currents, etc., are predicted at hundreds of thousands of grid boxes.

GCMs can be verified by comparing their output to the recent past, e.g., how simulated and observed temperatures changed over the 20th century. An exact match between observations and model simulations in a given period is not expected because of random fluctuations in the climate system. To overcome the influence of random fluctuations in climate, the output of an ensemble of model runs (as opposed to a single model run) is generally compared to observations.

All the GCMs used here have simulations for the 20th century. Annual minimum monthly winter temperatures (minimum[Dec, Jan, Feb, and Mar]) for the grid cell over southern Chesapeake Bay was extracted from the 20th century runs and compared with observed minimum winter temperatures for Virginia (http://www.sercc.com/climateinfo_files/monthly/Virginia_temp.html). As an example the GFDL CM2.1 mean was about 0.5°C lower and the standard deviation was slightly greater than observed (Table A2). The mean differences of other models ranged from +10°C to -4°C. These mean differences between the climate models and observations were used to bias correct the minimum winter air temperatures estimated by each GCM. The smoothed observations indicate a long-term cycle in minimum winter air-temperature with high temperatures in the 1940's and low temperatures in the 1970's; these warm and cool periods have been linked to the Atlantic Multidecadal Oscillation (Kerr 2000, 2005). Some of the modeled temperatures do not match this long-term trend in observed temperature, but the modeled temperatures seem to exhibit a cycle of similar duration and magnitude as observed.

Prior studies have shown that GCMs generally reproduce the continental-scale trends (Randall et al. 2007) and some regional trends (Knutson et al. 2006, Seager et al. 2007). For example, the GFDL CM2.1 reproduces the observed warming over the 20th century in the subtropical North Atlantic and continental U.S. when anthropogenic forcing is included, but

Table A1. List of General Circulation Models (GCMs) used in this study. The institution and model name are provided, as are the links to the model metadata. For each GCM, three scenarios were used: commit, B1, and A1B. In addition, a 20th century simulation was compared to 20th century observations to develop a mean bias correction for each model. All model outputs were downloaded from the World Data Center for Climate, IPCC Data Distribution Centre (http://www.mad.zmaw.de/IPCC_DDC/html/SRES_AR4/index.html)

Bjerknes Centre for Climate Research	BCM2.0
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=BCCR_BCM2.0_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CGCM3.1_T47_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=BCCR_BCM2.0_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=BCCR_BCM2.0_20C3M_1	
Canadian Centre for Climate Modeling and Analysis	CGCM3
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CGCM3.1_T47_COMMIT_2	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CGCM3.1_T47_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CGCM3.1_T47_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CGCM3.1_T47_20C3M_1	
Centre National de Recherches Meteorologiques	CM3
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CNRM_CM3_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CNRM_CM3_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CNRM_CM3_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CNRM_CM3_20C3M_1	
Australia's Commonwealth Scientific and Industrial Research	Mk3.0
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CSIRO_Mk3.0_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CSIRO_Mk3.0_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CSIRO_Mk3.0_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=CSIRO_Mk3.0_20C3M_1	
Meteorological Institute, University of Bonn	ECHO-G
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=ECHO_G_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=ECHO_G_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=ECHO_G_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=ECHO_G_20C3M_1	
Institute of Atmospheric Physics	FGOALS-g1.0
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=FGOALS_g1.0_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=FGOALS_g1.0_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=FGOALS_g1.0_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=FGOALS_g1.0_20C3M_1	
Geophysical Fluid Dynamics Laboratory	CM2.1
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GFDL_CM2.1_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GFDL_CM2.1_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GFDL_CM2.1_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GFDL_CM2.1_20C3M_1	

Goddard Institute for Space Studies	E-R
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GISS_ER_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GISS_ER_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GISS_ER_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=GISS_ER_20C3M_1	
Institute for Numerical Mathematics	CM3.0
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=INM_CM3.0_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=INM_CM3.0_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=INM_CM3.0_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=INM_CM3.0_20C3M_1	
Institut Pierre Simon Laplace	CM4
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=IPSL_CM4_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=IPSL_CM4_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=IPSL_CM4_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=IPSL_CM4_20C3M_1	
National Institute for Environmental Studies	MIROC3.2
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MIROC3.2_mr_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MIROC3.2_mr_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MIROC3.2_mr_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MIROC3.2_mr_20C3M_1	
Meteorological Research Institute	CGCM2.3.2
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MRI_CGCM2.3.2_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MRI_CGCM2.3.2_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MRI_CGCM2.3.2_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=MRI_CGCM2.3.2_20C3M_1	
National Centre for Atmospheric Research	CCSM3
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=NCAR_CCSM3_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=NCAR_CCSM3_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=NCAR_CCSM3_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=NCAR_CCSM3_20C3M_1	
UK Met. Office	HadCM3
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=UKMO_HadCM3_COMMIT_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=UKMO_HadCM3_SRESB1_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=UKMO_HadCM3_SRESA1B_1	
http://cera-www.dkrz.de/WDCC/ui/Compact.jsp?acronym=UKMO_HadGEM_20C3M_1	

over-estimates warming for the southeast US (Knutson et al. 2007). All climate models have biases and several factors may lead to model-data differences including model error, inadequate representation of regional processes (e.g., aerosol loading, deforestation/reforestation, irrigation), and natural variability (i.e., the atmospheric circulation over the southeast United States is influenced by El Nino and the Atlantic Multidecadal Oscillation). While there are differences between the GFDL CM2.1 and the observed annual temperature trends in the southeast U.S., there is general agreement between the simulated and observed minimum winter temperature in the GCMs considered here (Figure A1 and Table A2).

Table A2. Mean correction bias for each GCM. The average simulated minimum winter air temperature was compared to the average observed minimum winter air temperature over the 20th century. The difference in averages was added to the GCM simulated minimum winter air temperatures. A comparison of standard deviations is also provided.

Observed Minimum Winter Temperature		
	Mean	Standard Deviation
	0.65	2.00
Difference between observed and modeled temperatures		
GCM	Mean	Standard Deviation
BCM2.0	6.48	-0.59
CGCM3	-2.55	0.28
CM3	3.27	-0.37
MK3.0	-1.84	0.02
ECHO-G	2.75	-0.51
FGOALS g1.0	9.94	-0.44
CM2.1	-0.54	0.21
E-R	-3.71	0.28
CM3.0	2.78	-0.05
CM4	4.20	-0.08
MIROC3.2	8.79	-0.81
CGCM2.3.2	1.11	-0.42
CCSM3	3.06	-0.10
HadCM3	7.80	-0.10

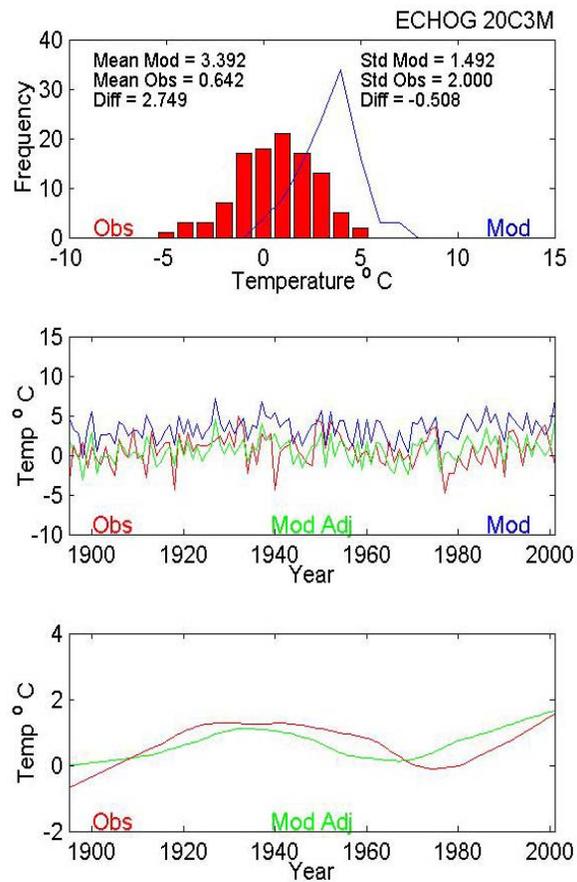
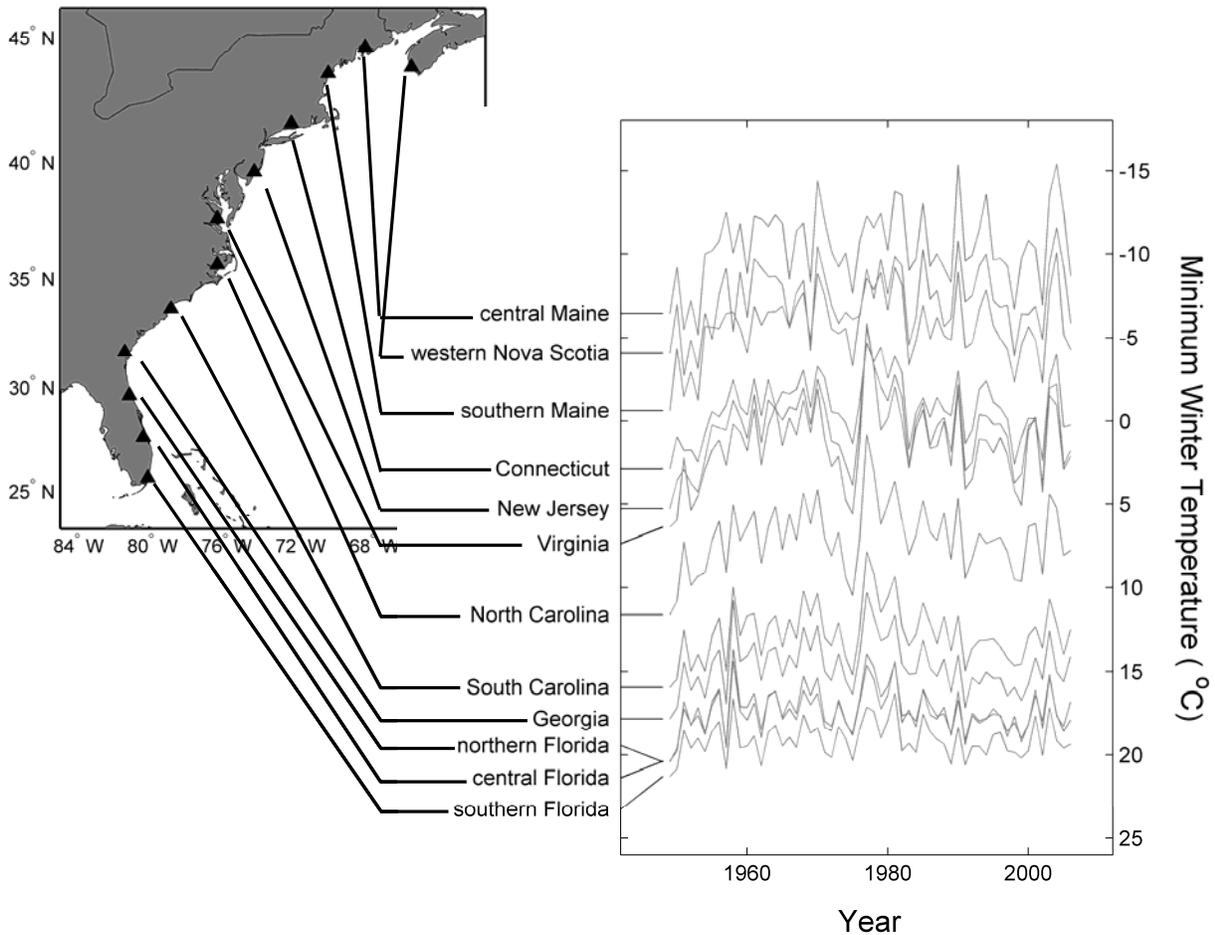


Fig. A1. Distributions of observed and modeled reanalysis minimum winter air temperatures and comparison of observed and predicted means and standard deviations of temperature (top row). Time series of observations and GCM predicted minimum winter temperatures. Also shown is the corrected model estimate based on adding the mean model-vs-observation difference to the model. Smoothed observations and predictions, with the predictions corrected by the mean difference between model and observations (bottom row). Results are shown for the ECHOG GCM; similar analyses were done for all GCMs. Observations are minimum monthly winter temperature in Virginia and model results are from the grid cell encompassing Chesapeake Bay.

Although, the analyses above suggest that the climate models reasonably capture the minimum monthly winter air temperatures in coastal Virginia, a potential concern is that the coupled climate-population model results are specific for this model grid cell. However, there is strong concordance in the time series of minimum winter air temperature over the eastern seaboard of the United States (Fig. A3) in historical observations and climate model hindcasts

Fig. A2. Time series of minimum winter air temperatures from the NCEP Reanalysis for grid cells nearest the locations indicated on the map. These data were significantly concordant: the pattern of interannual variability was coherent across the time series.



(Table A3). This concordance is expected since prior studies have documented strong concordance in interannual winter air temperature over the eastern U.S. (Joyce 2002), estuarine water temperatures in the mid-Atlantic (Hare and Able 2007), coastal water temperatures (Nixon et al. 2004), and sea surface temperature in the western North Atlantic (Friedland and Hare 2007). Additionally, minimum winter air temperature is closely related to minimum winter water temperature in estuaries along the mid-Atlantic coast (Hettler and Chester 1982, Hare and Able 2007) owing to the efficient heat exchange between atmosphere and water in these shallow systems (Roelofs and Bumpus 1953). Thus, minimum winter air temperatures from Virginia can serve as a proxy for coast-wide variability in minimum winter water temperatures.

2. Choice of a stock-recruitment function

A number of functions have been used historically to model the relationship between fish population size and subsequent recruitment (Hilborn and Walters 2004). There also are a number of extensions of these functions that include the effect of the environment on recruitment (Hilborn and Walters 2004). We evaluated two common stock recruitment functions (Beverton-

Holt and Ricker) and several extensions of these functions that include environmental effects (Table A4). The Akaike Information Criterion (AIC) was used to choose the best formulation to use in the coupled climate-population model. Spawning stock biomass and recruitment data were obtained from a recent stock assessment of Atlantic croaker (ASMFC 2005) and minimum winter air temperature in Virginia (http://www.sercc.com/climateinfo_files/monthly/Virginia_temp.html) was used as a proxy for water temperature during the estuarine juvenile stage (Hare and Able 2007).

The stock-recruitment functions were initially fit with non-linear algorithms, but these algorithms rarely converged. As a result, linear forms of the stock recruitment functions (model 1 and 4, see Table A4) were fit using least-squares regression. The environmental extensions of

the Ricker stock-recruitment model are easily linearized (models 5-11, see Table A4) and these models were also fit using least-squares. The environmental forms for the Beverton-Holt model (models 2 and 3) are not easily linearized. To fit these models, the standard Beverton-Holt terms (a and b) were estimated using the linearized version of the model (model 1), and then a non-linear fitting algorithm was used to estimate the environmental parameter (c) with the standard parameters (a and b) fixed at the appropriate values. Because the linearized forms of the models used different dependent variables ($1/R$ for Beverton and Holt and $\ln[R/S]$ for Ricker), AIC was estimated based on the models predictions of R using the non-linearized forms of the equations, with the terms derived from the linearized models. In this way, AIC was calculated based on the residual sums of squares of estimated R and observed R . The strength of evidence of the alternative models was calculated following (Burnham and Anderson 1998).

The Ricker stock-recruitment model with a temperature term was the best-supported model evaluated (Table A4), with the highest strength of evidence ($w=0.619$). The models with environmental terms were far superior to the standard stock-recruitment models. The relative likelihood of the environmental Beverton and Holt model (model 2) compared to the standard

Table A3. Kendall's concordance (W) for time series of minimum winter air temperatures from locations indicated in Fig. A3. Calculations were made for each of the models considered based on the 20th century runs. Kendall's concordance is a non-parametric test that measures the degree of agreement between multiple series of data: 0 indicates no agreement; 1 indicates perfect agreement. The NCEP/NCAR Reanalysis Product was also included in these analyses. This product is a gridded dataset based on retrospective observations (1948-2006) of a variety of atmospheric variables including surface temperature (Kalnay et al. 1996).

General Circulation Model	W	p	Years
NCEP Analysis	0.73	<0.001	1948-2006
BCM2.0	0.60	<0.001	1850-2000
CGCM3	0.62	<0.001	1850-2001
CM3	0.63	<0.001	1860-2000
MK3.0	0.61	<0.001	1871-2001
ECHO-G	0.59	<0.001	1860-2001
FGOALS g1.0	0.64	<0.001	1850-2000
CM21	0.61	<0.001	1861-2001
E-R	0.52	<0.001	1880-2004
HadCM3	0.58	<0.001	1860-2000
CM3.0	0.40	<0.001	1871-2001
CM4	0.67	<0.001	1860-2001
MIROC3.2	0.60	<0.001	1850-2001
CGCM2.3.2	0.67	<0.001	1851-2001
CCSM3	0.60	<0.001	1870-2000

Table A4. Akaike Information Criteria values for various models fit to stock (S) and recruitment (R) data for the mid-Atlantic stock of Atlantic croaker. Values provided for corrected Akaike Information Criteria (AIC_c), number of parameters in the model including the error term (k), the delta- AIC_c , which is scaled to the minimum observed AIC_c , and the model weights (w), which range from 0 to 1.

No	Model	Linearized Model	AIC_c	k	ΔAIC_c	W
1	$R = \frac{S}{b + aS}$	$\frac{1}{R} = a + \frac{b}{S}$	309.1	3	24.6	0.000
2	$R = \frac{e^{cT} S}{b + aS}$	Not linearized	291.5	4	7.0	0.019
3	$R = \frac{S}{b + e^{cT} aS}$	Not linearized	294.6	4	10.1	0.004
4	$R = Se^{a+bS}$	$\ln\left(\frac{R}{S}\right) = a + bS$	303.4	3	18.9	0.000
5	$R = Se^{a+bS+cT}$	$\ln\left(\frac{R}{S}\right) = a + bS + cT$	284.5	4	0.0	0.619
6	$R = Se^{a+bS+dT^2}$	$\ln\left(\frac{R}{S}\right) = a + bS + dT^2$	306.2	4	21.7	0.000
7	$R = Se^{a+bS+eST}$	$\ln\left(\frac{R}{S}\right) = a + bS + eST$	293.4	4	8.9	0.007
8	$R = Se^{a+bS+cT+dT^2}$	$\ln\left(\frac{R}{S}\right) = a + bS + cT + dT^2$	287.5	5	3.0	0.137
9	$R = Se^{a+bS+cT+eST}$	$\ln\left(\frac{R}{S}\right) = a + bS + cT + eST$	287.0	5	2.5	0.181
10	$R = Se^{a+bS+dT^2+eST}$	$\ln\left(\frac{R}{S}\right) = a + bS + dT^2 + eST$	295.8	5	11.3	0.002
11	$R = Se^{a+bS+cT+dT^2+eST}$	$\ln\left(\frac{R}{S}\right) = a + bS + cT + dT^2 + eST$	290.5	6	6.0	0.031

Beverton and Holt model was ~ 6000 to 1 ($w_{\text{model 2}} / w_{\text{model 1}}$). For the environmental Ricker (model 5) compared to the standard Ricker (model 4), the relative likelihood was ~ 10000 to 1. Based on these results, model 5 was chosen for use in the population model. Temperature-dependent Ricker models with higher order terms (model 8 and 9) had moderate strengths of evidence ($w=0.137$ and $w=0.181$). Model 8 includes a T^2 term, which could amplify the effect of warming on recruitment at higher minimum winter temperatures. However, over the range of temperatures forecasted in the climate models, the higher order models (model 8 and 9) predict very similar recruitment compared to the linear model (model 5), so non-linear effects are minimal, and thus these were not included in the final model.

3. Distribution model based on logistic regression

A multivariate regression approach was used to model distribution as a function of population size and winter temperature. The hypothesis was that as population size increased and winter temperatures increased the mean and northern extent of the population (mean + 2 standard deviations) would shift northward. A shift in mean location is not necessarily predicted with increasing population size; the mean could remain stationary and the northern and southern extents of the population could expand. However, in the case of Atlantic croaker, sampling did not occur throughout the range of the population; sampling stopped at a fixed geographic location, so an expansion in the southern range would not be observed. Thus as the northern range extends and the southern boundary of sampling remains stationary a northward shift in the mean location is predicted.

As an alternative approach to multiple regression for modeling distribution, a logistic regression was developed that used the presence / absence at individual trawl stations. First, trawl stations were screened to remove stations that sampled deeper than 45 m; this value was based on the 5% level of a logistic regression of catch on depth. The logistic regression model was used in a form similar to the average distance model. Catch at station s in year Y was modeled as the distance of station s in year Y , spawning stock biomass (S) in year Y , and minimum winter temperature in year Y :

$$catch_{sY} = a + b \cdot dist_{sY} + c \cdot SSB_Y + d \cdot T_Y + e \cdot SSB_Y^2 + f \cdot T_Y^2 \quad (6)$$

The model was fit using the `glm [family=binomial(link="logit")]` function in R (<http://www.r-project.org/>) and an Akaike multi-model inference was used to determine the model parameters. The model was then used to forecast Atlantic croaker distribution estimating the distance to the 50% and 10% catch probability. The results were qualitatively similar to those from the average distance approach, with distances decreasing with increasing F and increasing with increasing CO_2 emissions; we choose to present the results of the multiple regression model.

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