

Rebuilding in the face of climate change

Richard J. Bell, Anthony Wood, Jonathan Hare, David Richardson, John Manderson, and Timothy Miller

Abstract: Decadal-scale climate variability and change can cause trends in oceanographic conditions that impact demographic rates. Rebuilding scenarios, therefore, developed assuming constant demographic rates may not be realistic. Winter flounder (*Pseudopleuronectes americanus*) is an important commercial and recreational species that has declined in the southern portion of its range despite reduced exploitation. Laboratory and mesocosm studies suggest that stock productivity is reduced under warmer conditions and that rebuilding to historical levels may not be possible. Our goal was to examine the rebuilding potential of winter flounder in the face of regional warming. We integrated winter temperature into a population model to estimate environmentally driven stock–recruitment parameters and projected the stock into the future under different climate and fishing scenarios. The inclusion of winter temperature had minor impacts on the estimates of current abundance, but provided greater understanding of the drivers of recruitment. Projections that included the environment suggest that rebuilding the stock to historical levels is unlikely. The integration of both fishing and the environment has the potential to provide more realistic expectations of future stock status.

Résumé : La variabilité et les changements climatiques décennaux peuvent produire des tendances dans les conditions océanographiques qui influencent les taux démographiques. Aussi, les scénarios de reconstitution élaborés en présumant des taux démographiques constants pourraient ne pas être réalistes. La plie rouge (*Pseudopleuronectes americanus*), une espèce importante pour la pêche commerciale et sportive, est en baisse dans la partie sud de son aire de répartition, malgré une réduction de son exploitation. Des études en laboratoire et en mésocosme donnent à penser que la productivité du stock diminue dans des conditions plus chaudes et que le rétablissement des niveaux historiques pourrait ne pas être possible. Notre objectif consistait à examiner le potentiel de reconstitution du stock de plie rouge étant donné le réchauffement régional. Nous avons incorporé la température hivernale dans un modèle de population afin d'estimer les paramètres de recrutement au stock modulés par des facteurs ambiants et avons établi des projections du stock pour différents scénarios climatiques et de pêche. L'intégration de la température hivernale a des effets mineurs sur les estimations de l'abondance actuelle, mais permet une meilleure compréhension des facteurs qui modulent le recrutement. Les projections qui intègrent les conditions ambiantes indiqueraient que le rétablissement des niveaux historiques du stock est improbable. L'intégration de la pêche et des conditions ambiantes pourrait produire des prévisions plus réalistes de l'état futur du stock. [Traduit par la Rédaction]

Introduction

With the reauthorization of the Magnuson–Stevens Act, rebuilding plans were implemented in the United States to provide a legally binding time line to reduce overfishing (NOAA 1996). For many species along the US Northeast Shelf, fishing pressure was the major driver controlling stock status, and regulating fishing mortality has led to recovery (e.g., haddock (*Melanogrammus aeglefinus*), summer flounder (*Paralichthys dentatus*), scup (*Stenotomus chrysops*), striped bass (*Morone saxatilis*), Acadian redfish (*Sebastes fasciatus*); NRC 2014). Fishing pressure, however, is not the only driver of stock abundance, as exemplified by the response of small pelagics to decadal-scale forcing such as El Niño Southern Oscillation events (Baumgartner et al. 1992; Chavez et al. 2003). Oceanographic conditions vary in time and space and modulate intrinsic rates such as growth, mortality, and fecundity, which in turn affect the dynamics of the stock (Manderson 2016). As fishing pressure has declined, the relative importance of the environment on driving changes in productivity and natural mortality has had an increased effect on natural marine resources (Hare et al. 2010). The Magnuson–Stevens Act specifically recognizes

the importance of nonanthropogenic factors and indicates that reference points should reflect the prevailing environmental condition.

Owing to increased model complexities, a lack of strong mechanistic links between the environment and stock-specific rates that hold up over time, and often insufficient data, climate variables are rarely included in stock assessments and management (Myers 1998; Skern-Mauritzen et al. 2016). Many assessment models incorporate variability and uncertainty by estimating parameters as white noise about a mean when possible, but due to the difficulties of estimating numerous parameters with short time series and limited data, most parameter estimates are constant over time or fixed (Quinn and Deriso 1999; Szuwalski and Hollowed 2016). The mean parameter estimates, however, typically produce reasonable estimates of the current biomass, particularly in age-structured assessments. Fishing, then, largely becomes the only time-varying parameter that has an influence on stock status. Projections into the future and rebuilding scenarios with reduced fishing mortality, therefore, generally show population growth. Projections do account for the uncertainty in parameter esti-

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mates, but typically do not account for the potential variability due to the environment or species interactions that can be red noise, with autoregressive properties (Steele and Henderson 1984; Steele 1985).

Recruitment variability is an important aspect of forward projections, and annual estimates are often randomly selected from the empirical data or a theoretical distribution (Hennemuth et al. 1980; Brodziak et al. 1998; Brodziak and Rago 2008). The median future recruitment over thousands of simulated projections, however, is typically stationary with the width of the confidence intervals being dependent on the range of values that went into the input. Stationary, median recruitment puts constraints on stock productivity and results in fishing being the main factor driving stock trends.

Around much of the globe, the climate is changing, and temperatures are predicted to increase due to anthropogenic carbon emissions (IPCC 2013). Species at the edge of their range often experience greater impacts as interannual, and seasonal changes in the physical conditions cause their geographic location to shift between suitable and unsuitable habitat (Travis and Dytham 2004; Hampe and Petit 2005; Bates et al. 2014). In the Northern Hemisphere, stocks at the southern extent of their range are likely to experience warmer conditions that could impact their intrinsic rates and reduce productivity leading to a decline in abundance (Hampe and Petit 2005; Holt and Punt 2009; Nye et al. 2009; Pinsky et al. 2013). However, at the northern extent of their range, habitat quality may increase leading to increased productivity (Beaugrand and Kirby 2010; Bates et al. 2014). It is at these marginal habitats, the limits of a species range, that the environment is likely to have its greatest influence on stock dynamics and be simple enough to understand (Myers 1998).

We sought to examine the impact of climate variability and change on fisheries rebuilding plans. As a test case, we used the Southern New England – Mid-Atlantic (SNE–MA) stock of winter flounder (*Pseudopleuronectes americanus*). SNE–MA winter flounder is at the southern extent of its range and has declined over the last 30 years (NEFSC 2011). Winter flounder are a cold-water species, and the coastal stock enters bays and estuaries in the winter to spawn (Collette and Klein-MacPhee 2002). The eggs and larvae develop during the coldest time of the year, and there is a working hypothesis that the low temperature (<6 °C) creates a thermal refuge from predation (Jeffries and Johnson 1974). Lab and mesocosm studies have found increased predation in warmer waters (Keller et al. 1999; Taylor and Collie 2003), and coast-wide recruitment has been linked to broad-scale environmental conditions (Bell et al. 2014; Manderson 2008). In 2010, it was estimated that the spawning stock biomass (SSB) of SNE–MA winter flounder was ~16% of its SSB_{MSY} (i.e., the level of spawning stock biomass that can enable maximum sustainable yield) reference point and had a less than 1% chance of achieving its biomass target by the 2014 rebuilding date (NEFSC 2011). To allow time for recovery, the rebuilding date was changed to 2023 (NEFMC 2009, 2013).

Our goal was to examine rebuilding potential in the face of climate change. We are not attempting to conduct an independent stock assessment of SNE–MA winter flounder, but simply exploring the ways in which different assumptions about the impact of the environment and fishing pressure could affect rebuilding to the current reference points from the SNE–MA winter flounder stock assessment (Holt and Punt 2009; NEFSC 2015). As an exploratory exercise, we incorporated winter estuarine temperature into a winter flounder population model to estimate temperature-dependent recruitment parameters. The temperature-dependent recruitment parameters could then be used with cli-

mate model output to project the SNE–MA stock forward in time under different fishing scenarios.

Methods

A standard and an environmentally driven age-structured population model were fit to the catch and survey data of SNE–MA winter flounder. Estuary water temperature was incorporated into the stock-recruitment relationship within the environmentally driven model. The output of each model was projected to 2050 with estimates of temperature derived from an ensemble of earth system models from the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC 2013). The ability of SNE–MA winter flounder to rebuild to its current biomass reference point was assessed under three fishing scenarios: (1) no fishing ($F = 0$), (2) moderate fishing representing a small fishery and (or) incidental catch ($F = 0.1$), and (3) fishing at the current reference level to achieve MSY ($F = F_{\text{MSY}} = 0.325$; NEFSC 2015).

Temperature

Historical, weekly estuary water temperature time series were compiled for five estuaries covering the range of the Southern New England–Mid-Atlantic winter flounder stock: Woods Hole, Massachusetts (Nixon et al. 2004); Narragansett Bay, Rhode Island (Collie et al. 2008); Long Island Sound (Milford Laboratory, National Oceanic and Atmospheric Administration (NOAA)); Delaware Bay (Susan Ford, Haskin Shellfish Research Laboratory); and Chesapeake Bay (Gary Anderson (VIMS 2003)). A model linking historical air temperature to historical estuary temperature was used to fill in gaps (see Bell et al. (2014) for details). The mean weekly temperature from January through March for each estuary was averaged to produce the annual winter estuary temperature. The mean water temperature across each estuary was included as the environmental driver in the population model. Air temperature over the east coast of the United States is highly coherent (Hare et al. 2010; Joyce 2002), resulting in estuary water temperatures that are highly coherent and strongly correlated with air temperature (Bell et al. 2014; Hare et al. 2012b).

The output of 14 earth system models that were part of the IPCC AR5 (IPCC 2013) were obtained through the Coupled Model Inter-comparison Project Phase 5 (CMIP 2017; see online Supplementary material, Table S1¹ for a list of the models). The variable of interest was near-surface air temperature (tas) from the monthly mean atmospheric fields and some surface fields (Amon). One ensemble member (r1i1p1) was obtained for Historical and Representative Concentration Pathway 8.5 (RCP8.5) runs from each model; RCP8.5 represents a “business-as-usual” scenario. The climate forecast delta method was used to bias correct the climate models. The regridded hindcast model runs were compared with observed winter-estuary temperatures to calculate a delta for bias correcting the future projections (Stock et al. 2011). For each grid cell corresponding to the estuaries, a winter mean (January, February, and March) of the hindcast model surface air temperature over the period 1985–2004 was calculated. Similarly, the January, February, and March observed winter-estuary temperature over the period 1985–2004 were averaged (Bell et al. 2014). The difference between these observed and modeled averages for each of the 14 earth system models (termed deltas) were used to bias-correct each of the climate model projections. Annual projections from each of the 14 earth system AR5 models were calculated. The mean of the January, February, and March delta-corrected air temperatures from the AR5 earth system models were averaged over the Northeast US coast grid cells to produce 14 annual estimates of winter-estuary temperature projected to 2050. The biomass pro-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0085>.

jections were conducted with each of the 14 future temperature time series. The biomass estimates of the 14 different projections were averaged together to produce a mean biomass estimate for the temperature-dependent scenarios.

Population model

The winter flounder population values were estimated with the Age Structured Assessment Program model version 2 (ASAP v.2; Legault and Restrepo 1998; Legault 2008). Two models were run, one with and one without an environmentally driven stock-recruitment function. The environmental ASAP (ASAP_E) model was a modified version of the standard ASAP v.2 (Miller 2012). The environmentally driven stock-recruitment function option is currently part of the latest version of ASAP. All the input data (e.g., catch-at-age, survey abundance-at-age, weight-at-age, maturity) were taken from the most recent winter flounder stock assessment (NEFSC 2015).

ASAP is a forward projection age-structured population model available from the NOAA toolbox (NOAA Fisheries Toolbox 2008). The recruits in each year (R_t) are estimated from a Beverton–Holt stock-recruitment relationship formulated with steepness (h) and unexploited recruitment (R_0) (Mace and Doonan 1988). The standard Beverton–Holt relationship combines the SSB with two parameters, stock productivity (α) and compensation (β), to calculate the number of recruits. The Mace and Doonan (1988) formulation uses h and an estimate of R_0 , the level of recruitment from the unfished or unexploited spawning stock biomass (SSB₀), or the unexploited spawner-per-recruit ($SPR_0 = SSB_0/R_0$). Steepness (h) is a proportion, calculated as the level of recruitment at 20% of SSB₀ divided by R_0 ($h = R_{SSB_{20\%}}/R_0$). SPR_0 is a function of weight-at-age, maturity-at-age, and natural mortality.

$$(1) \quad R_t = \frac{\alpha SSB_{t-1}}{\beta + SSB_{t-1}} = \frac{4hR_0SSB_{t-1}}{SSB_0(1-h) + (5h-1)SSB_{t-1}}$$

The environmental population model (ASAP_E) included a time-varying unexploited recruitment parameter ($R_{0,t}$) that is a function of the environmental covariate (x_t). SSB₀ was therefore replaced with SSB_{0,t} = $SPR_0 \cdot R_{0,t}$.

$$(2) \quad R_{0,t} = e^{\beta_0 + \beta_1 x_t}$$

Previous work (Bell et al. 2014) modified the stock productivity term (α) of the standard Beverton–Holt curve with temperature. The α term is a function of both h and R_0 in the Mace and Doonan (1988) formulation in ASAP, and we modified R_0 with temperature. Within ASAP, the age-1 abundance is not simply the recruits predicted from the stock-recruitment relationship. ASAP estimates recruitment (the numbers at age-1: $\hat{N}_{a=1,t}$) as deviations from the stock-recruitment predicted recruitment.

$$(3) \quad \hat{N}_{a=1,t} = R_t e^{\delta R_t}$$

A lognormal penalty for each recruitment deviation (δR_t) is added to the objective function in ASAP where the coefficient of variation (CV) of the deviations is user-specified. Larger CV down-weights the penalty relative to data components or other components of the objective function. If the δR_t are large or have a strong pattern, it indicates that the recruits are not following the Beverton–Holt stock-recruitment relationship and suggests that recruitment is being driven by processes in addition to the magnitude of SSB. External environmental drivers (Fogarty et al. 2008; Hare and Able 2007), variability in spawner conditions (Leaf and Friedland 2014), predator–prey interactions (Minto and Worm 2012), and sto-

chastic variability (Quinn and Deriso 1999) have all been indicated as potential factors in the spawner–recruit relationship.

The standard and environmental population models were run to estimate the parameters used for the rebuilding projections and to investigate the impact of an environmental covariate on the estimates of biomass and abundance. In the standard population model, the CV of the δR_t was large (CV = 0.5), resulting in age-1 abundances that were basically unconstrained by the stock-recruitment relationship. The large CV essentially created a model in which the raw data drove the age-1 estimates without regard to the Beverton–Holt stock-recruitment relationship. The environmental model included a time-varying $R_{0,t}$ term that was a function of the winter temperature environment covariate. The CV of the recruitment deviations was specified at two different values (CV = 0.2 and 0.5). The large CV (CV = 0.5) had the same assumption as the standard model, assuming little to no relationship between SSB and recruitment, and the smaller CV (CV = 0.2) constrained the estimated age-1 to deviate little from the environmentally driven stock-recruitment relationship. The smaller CV assumed there was a stock-recruitment relationship, and deviations from the standard Beverton–Holt model were largely driven by temperature. Only the CV of the recruitment deviations was fixed. All the parameters were estimated within the model.

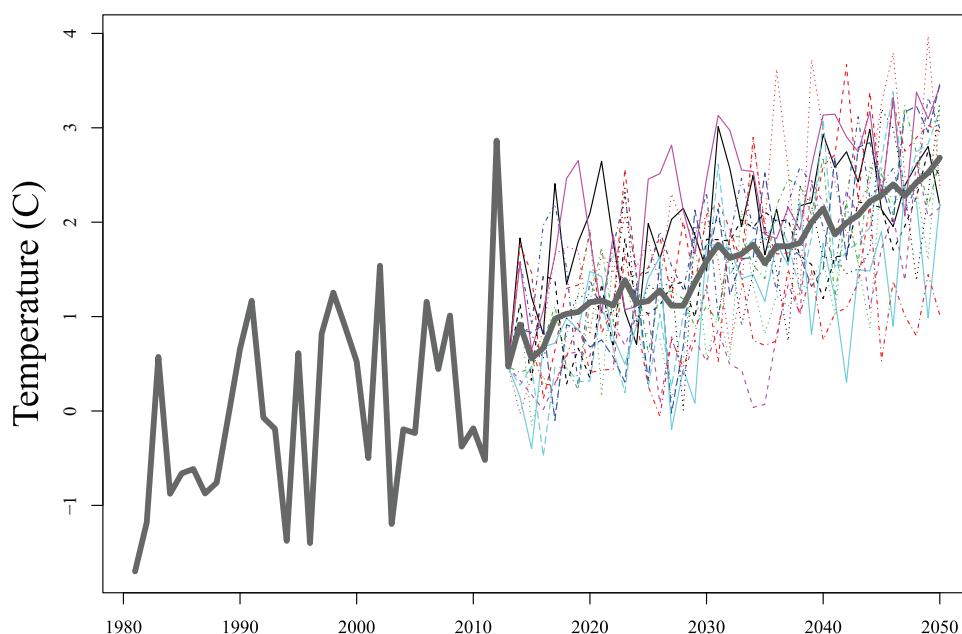
Projections

Stochastic forward projections for the age-structured population were performed in the AGEPRO (Age Structured Projection Model) software program available from the NOAA toolbox (NOAA Fisheries Toolbox 2008). We used the ASAP model to obtain 1000 draws from the joint sampling distribution of the maximum penalized likelihood estimates by retaining every 200th parameter set of a chain of 200 000 iterations produced by Markov chain Monte Carlo (MCMC) on the penalized likelihood. This distribution is equivalent to a Bayesian posterior distribution that implicitly assumes improper uniform priors for all parameters except the recruitment deviations, which is defined by the stock-recruitment penalty (Stewart et al. 2013). Aside from the stock-recruitment penalty, the properties of these estimates are asymptotically equivalent to a joint normal distribution with mean and variance defined by the maximum likelihood estimate and the inverse Hessian of the negative log-likelihood, respectively. We used the values of abundance-at-age in 2013 from this distribution as the input to AGEPRO due to the greater uncertainty in abundance, particularly of recruitment, in the terminal year (2014). Winter flounder biomass was projected from 2013 to 2050 with AGEPRO under three environmental–recruitment hypotheses and three fishing scenarios.

The three recruitment scenarios were as follows: (1) BASE projection — over the course of the historical time series there had been no change in the productivity of the winter flounder stock; (2) ENVIRON projection — over the course of the historical time series there had been a change in the productivity of the winter flounder stock, but any environmental relationship between SSB and recruitment was unknown; (3) TEMP projection — over the course of the historical time series there had been a change in the productivity of the winter flounder stock and there was a temperature-dependent relationship between SSB and recruitment (Bell et al. 2014).

The three different environmental–recruitment hypotheses were modeled in AGEPRO with three different recruitment model formulations: (1) BASE projection — with the assumption of no change in productivity, abundance was projected with a standard Beverton–Holt stock-recruitment model that was used in the stock assessment for short-term projections (NEFSC 2015). (2) ENVIRON projection — with the assumption of changes in productivity over time, the most recent years of the time series were considered the best representation of the future condition of winter flounder. An empirical recruitment model was used in which there was no relationship between SSB and recruitment

Fig. 1. The observed historical temperature time series (1981–2013), along with the delta-corrected temperature projections of the 14 AR5 earth systems models and the ensemble mean (2014–2050). The peak in 2012 is the true 2012 winter estuary temperature. [Colour online.]



(Brodziak et al. 1998; Szuwalski et al. 2015). Recruitment for each year in the projection was randomly selected from the entire time series of the estimated age-1 abundance from ASAP (1981–2013). The probability of selecting a particular estimate of age-1 abundance from ASAP was skewed, however, such that the most recent years had a higher probability of being selected (Fig. S1¹). Weight-at-age, fishing selectivity by age, natural mortality, and maturity-at-age were the mean of the last 5 years: 2009 to 2013. (3) TEMP projection — with the assumption of temperature-dependent changes in productivity, the future condition of winter flounder was considered a direct function of future temperature. Recruitment was projected with a temperature-dependent Beverton–Holt stock–recruitment model. The α and β parameters were calculated from the temperature-modified R_0 parameter from the ASAP_E population model (CV = 0.2). Steepness, estimated from the ASAP_E population model, was used, and the mean of the SPR_0 value from 2009–2013 was used to calculate SSB_0 . Weight-at-age, fishing selectivity by age, natural mortality, and maturity-at-age were the mean of the last 5 years: 2009 to 2013.

Three fishing scenarios were examined: (1) no fishing ($F = 0$), (2) moderate fishing representing a small fishery and (or) incidental catch ($F = 0.1$), and (3) fishing at the current reference level to achieve MSY ($F = F_{MSY} = 0.325$; NEFSC 2015). The rebuilding target was the SSB_{MSY} from the official stock assessment ($SSB_{MSY} = 26\,928$ t; NEFSC 2015). The current fishing reference point (F_{MSY}) was generated from a Beverton–Holt stock–recruitment relationship as part of the official stock assessment process (NEFSC 2015). The SSB_{MSY} reference point was developed from a proxy based on long-term stochastic projections for the assessment (NEFSC 2015).

Results

Temperature

The projected temperature increased over the next half century (Fig. 1). The variability in each individual projection was similar to historical observed values and was used for the TEMP projections. The variability of the ensemble mean, however, was lower than that of observed values.

Population model

The standard and the environmental population models converged and produced qualitatively similar results (Fig. 2). There was reasonable agreement between the catch-at-age and survey-abundance-at-age data, which constrained the estimates of SSB, recruitment, and F for the different models.

The total value of the objective function for each model was similar, with the environmental model (CV = 0.5) having a lower value than the standard model (Table 1). The objective function values are comparable across models with the same CV. The values for the environmental model (CV = 0.2) were included for completeness. The objective function components for observed versus predicted abundance-at-age for the multiple surveys were very similar, as were the year 1 abundances. The δR_t component of the objective function was larger in the standard model compared with the environmental model (CV = 0.5). The root mean square error terms (RMSE) for most components were very similar among the models (not all components listed); however, there were differences among some of the recruitment diagnostics, with certain components being closer to the optimal value of one in the standard model and other components closer to one in the environmental models ($RMSE = \sqrt{\text{mean}(\text{residuals}^2)}$). All three models, however, produced a reasonable representation of the data.

The three models have a divergence starting in the mid-1990s in which SSB was lower for the environmental models and fishing mortality was higher. The outputs were similar, but were considered significantly different based on a parametric bootstrap (see Supplemental material¹). The largest difference between the standard and environmental models was the vector of δR_t (Fig. 2). The deviations in the standard model exhibited a clear declining trend over time, indicating that the standard Beverton–Holt model did not represent the data well. During the early part of the time series, recruitment was above the stock–recruitment model predictions based on SSB and toward the end of the time series was below model predictions. The temperature-dependent stock–recruitment relationship accounted for some of the variability in the recruitment deviations and suggests that stock productivity may be tied to winter estuary temperatures. The declining trend in δR_t was reduced in the environmental model with CV = 0.5,

Fig. 2. The estimated spawning stock biomass (SSB), recruitment, fishing mortality and lognormal deviations from the standard population model and the two environmentally driven population models (recruitment coefficient of variation = 0.2 and 0.5). The confidence envelopes are one standard deviation. [Colour online.]

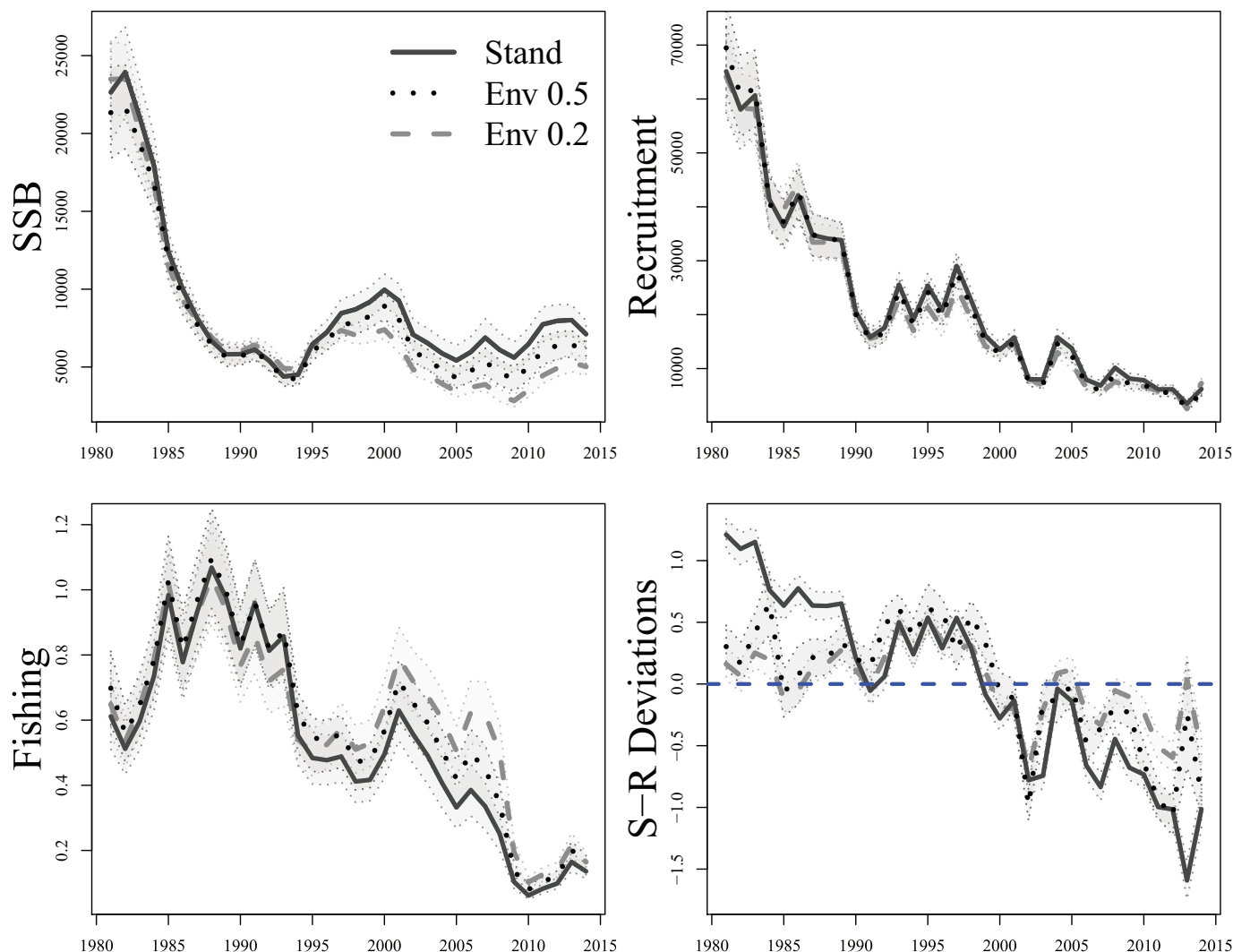


Table 1. The magnitude of the objective function and the root mean square error (RMSE) for specific components of the standard model, coefficient of variation (CV = 0.5), and the two environmental models (CV = 0.5 and 0.2).

	ASAP _{Stand}	ASAP _{0.5}	ASAP _{0.2}
Objective function	4180.3	4155.64	4174.28
Survey age comparisons	3648.81	3644.15	3635.36
$N_{a=1}$	63.6046	63.0843	63.9203
δR_t	12.8241	-8.20357	-17.4427
h	0	-1.79082	-0.110475
RMSE			
$N_{a=1}$	1.36656	0.352673	0.294081
δR_t	1.50143	1.00865	1.48745

Note: Components include the overall objective function, the comparisons of the numbers at age, the numbers at age-1 ($N_{a=1}$), the deviations in recruitment (δR_t), and steepness (h). Objective function values with different CVs are not directly comparable. ASAP, Age Structured Assessment Program.

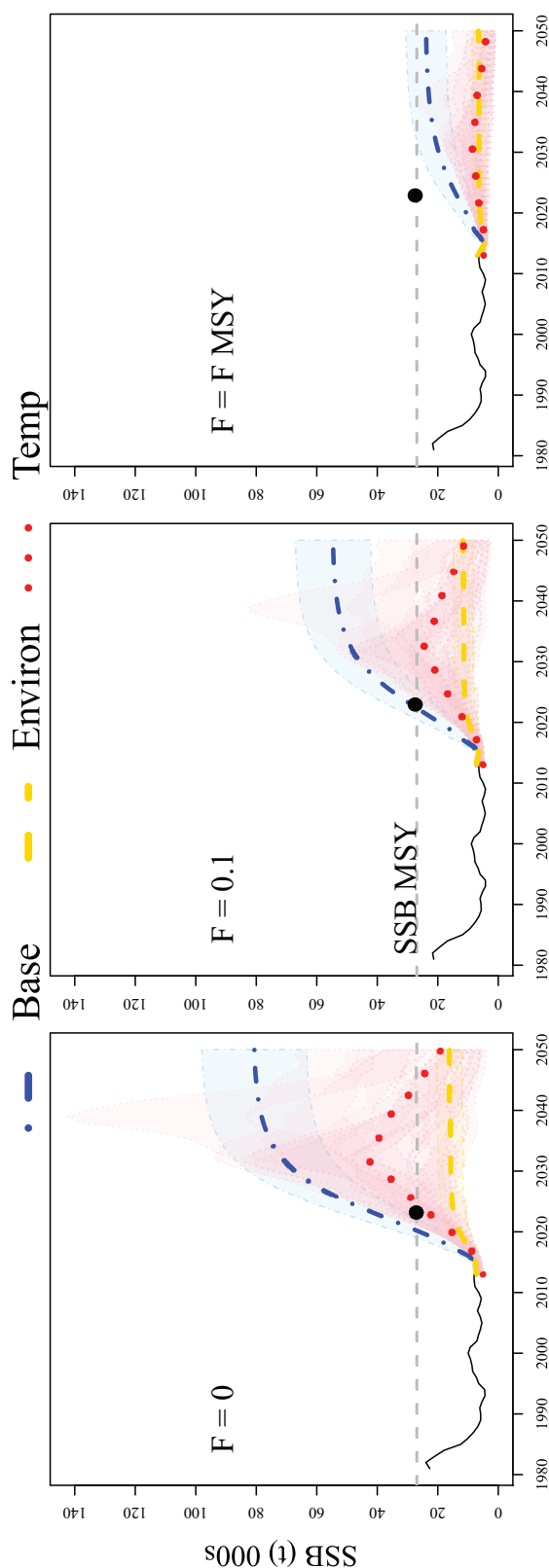
particularly in the early part of the time series, and was further reduced in the environmental model with CV = 0.2. The smaller magnitude of the deviations was due to the tighter CV (0.2), and the increasing trend in winter-estuary temperature accounted for much of the declining trend in the δR_t present in the standard

model. The environmental models did not account for all the variability, however, and there appeared to be a change in the relationship around 2000 and (or) the potential addition of compounding factors.

Projections

Under all the future environmental and fishing scenarios, SSB increased, at least in the short term (Fig. 3). The BASE projection did not include an environmental factor and was driven by fishing and stochastic processes. The reduction in fishing reduced overall mortality and abundance increased. Under the no fishing scenario, the median SSB surpassed the previously established rebuilding target and was larger than historical estimates. With increasing fishing, median SSB was reduced, but still attained SSB_{MSY} with limited fishing pressure ($F = 0.1$); however, it did not rebuild fully at the F_{MSY} level within the time frame of the projection. The different AR5 temperature projections produced a range of SSB values for the TEMP runs, with two projections producing estimates that were of similar magnitude to the BASE run. The mean SSB across the 14 projections was substantially lower, however. The median SSB increased initially in the ENVIRON and TEMP runs before leveling off or declining. The median SSB reached the current reference point in the TEMP projection, but only for a short time and was reduced under the different fishing

Fig. 3. The estimated and projected spawning stock biomass (SSB) under different fishing rates and environmental assumptions. The black line is the estimated SSB through 2013. The three projections represent the BASE run (no change in productivity), the ENVIRON run (changes in productivity with unknown drivers), and TEMP run (temperature-dependent changes in productivity). The horizontal grey dashed line is the estimated SSB at maximum sustainable yield (SSB_{MSY}). The black dot is the 2023 rebuilding target. [Colour online.]



scenarios. The median SSB increased in the TEMP projection until the 2030s and then declined with increasing temperatures.

In the projection models, recruitment, fishing, and stochasticity are the main factors that regulate abundance. Natural mortality, as well as weight and maturity-at-age, are also important, but are the same or similar in the different projections. When fishing is restricted, SSB increases, which drives an increase in recruitment for the BASE and TEMP projections, at least initially (Fig. 4). In the ENVIRON projection model, recruitment is not linked to SSB and is based on the historical estimates from the population model. The median recruitment is therefore stationary and does not vary with changes in fishing or SSB (Fig. 4). Median recruitment was roughly 12 million throughout the projection. The effect of temperature reduces mean recruitment in the TEMP runs compared with the BASE run, though two projections that include temperature are of similar magnitude to the BASE run. Recruitment is lower in the TEMP runs, but does not result in an actual decline in recruitment until the late 2020s. The declining mean recruitment reduces SSB, regardless of fishing, and does not make it possible to maintain SSB_{MSY}.

The catch was largely dictated by the fishing level (Fig. 5). Stationary median SSB in the ENVIRON projection resulted in stationary median catch. SSB declined in the TEMP projection due to temperature, resulting in reduced catch after about 2030, and none of the projected catch levels matched the large catches removed in the early 1980s.

Discussion

Rebuilding targets provide a legally binding time line for increasing the population of depleted species. In the United States, the number of overfished stocks has decreased substantially since the reauthorization of the Magnuson–Stevens Act in 1996 (NMFS 2015; NOAA 1996). The required firm catch quotas have enabled a number of stocks to recover or make progress toward recovery, but not all. The lack of improvement, despite the reduction in fishing mortality, suggests additional drivers beyond fishing pressure can also impact the abundance of natural marine resources (A'mar et al. 2009; Link 2010; Perry et al. 2010; Hollowed et al. 2013). Ecosystem factors such as climate variability and change can affect stock productivity, which in turn impacts rebuilding time lines (Sinclair and Crawford 2005; Hollowed et al. 2009; Holt and Punt 2009; Holsman et al. 2016).

The inclusion of climate factors can provide valuable information about the drivers of stock dynamics, but may not make substantial changes to the estimates of abundance. Where there are good data, population models with time-invariant parameters often produce good estimates of stock abundance (McKenzie 2016). As was seen from this example, the high-quality data available on the US Northeast Shelf produced estimates of abundance that were similar with and without the inclusion of an environmental parameter. The differences were the result of a change to a more dome-shaped selectivity in the mid-1990s and a slightly higher estimate of SSB productivity in the environmental models. Fishing mortality increased in the environmental models, particularly on the oldest age classes, reducing the SSB to produce similar estimates of recruitment across all three models that would agree with the age composition data. In marine systems, the environment typically has its greatest influence on the early life stages of organisms (Houde 1987) and is therefore often incorporated into the recruitment function of population models, enabling time-varying effects in productivity (Quinn and Deriso 1999). In age-structured population models, the catch-at-age and survey-at-age data constrain the estimates of plausible recruitment and subsequent estimates of the population age structure. The environment is not explicitly included, but variable recruitment, which may or may not be the result of environmental conditions, is an output of age-structured models.

Fig. 4. The estimated and projected recruitment under different fishing rates and environmental assumptions. The three projections represent the BASE run (no change in productivity), the ENVIRON run (changes in productivity with unknown drivers), and TEMP run (temperature-dependent changes in productivity). [Colour online.]

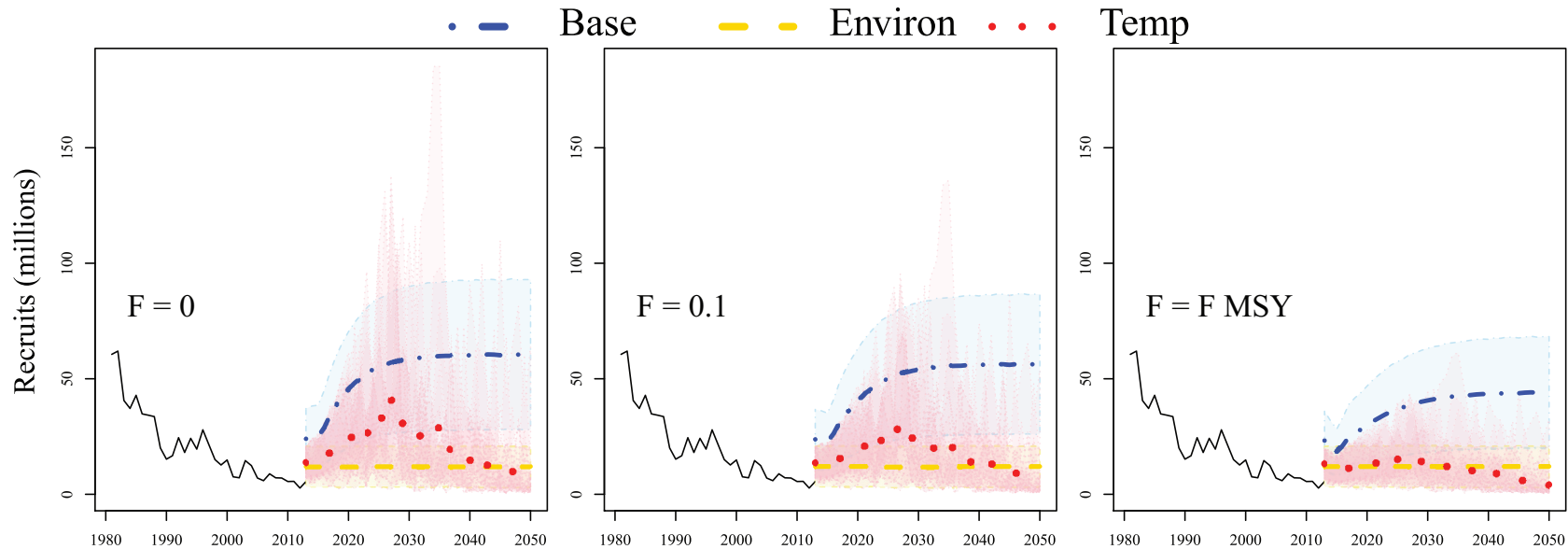
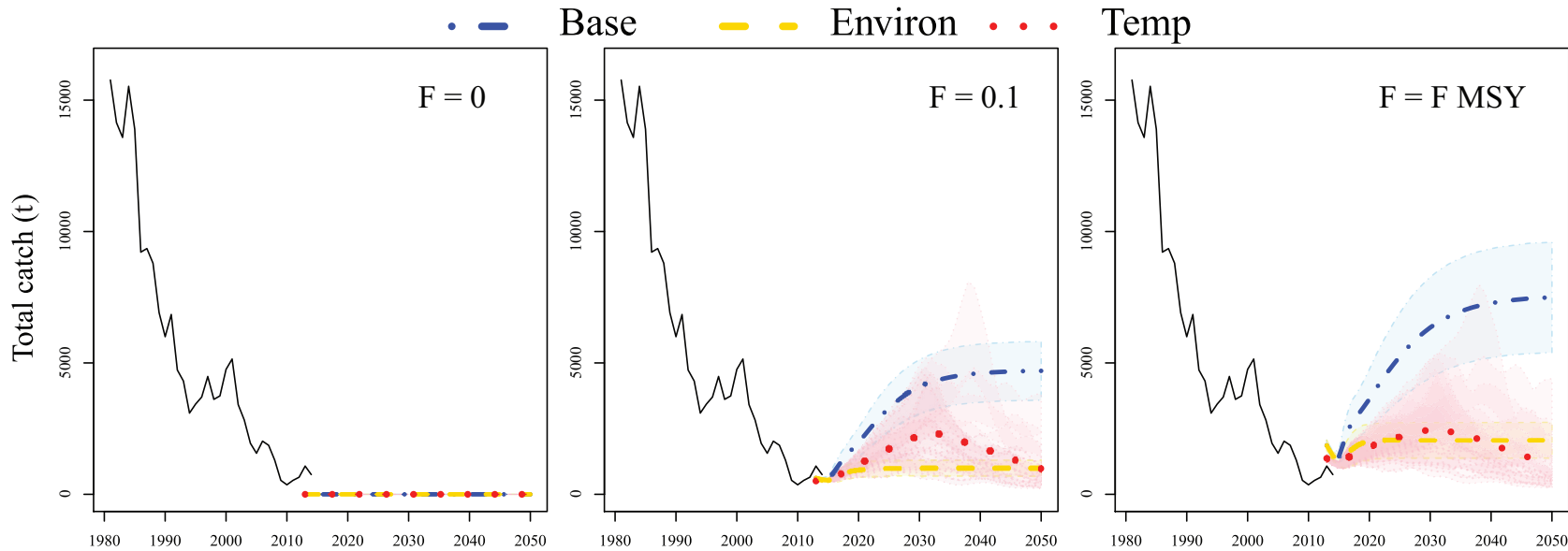


Fig. 5. The true and projected catch under different fishing rates and environmental assumptions. The black line is the true catch through 2013. The three projections represent the BASE run (no change in productivity), the ENVIRON run (changes in productivity with unknown drivers), and TEMP run (temperature-dependent changes in productivity). [Colour online.]



An environmentally driven model, however, may provide some insight into factors regulating abundance and a better understanding of how those factors will impact a stock in the future (Maunder and Watters 2003; A'mar et al. 2009; Holt and Punt 2009; Sagarese et al. 2015). In our winter flounder example, there is evidence that winter conditions are driving changes in productivity. Warmer winter estuarine temperatures enabled greater predation on the early life stages, decreasing the number of recruits expected per spawner from the stock–recruitment relationship (Jeffries and Johnson 1974; Keller and Klein-MacPhee 2000; Taylor and Collie 2003; Bell et al. 2014). The largest difference between the standard model and the environmental models was the deviations in recruitment (δR_t). Though recruitment in the standard model was largely unconstrained with little to no stock–recruitment relationship, the estimated recruitment values exhibited a strong declining temporal trend in the deviation from the Beverton–Holt stock–recruitment model. In the environmental models (constrained: CV = 0.2; and unconstrained: CV = 0.5), the temperature covariate accounted for much of the recruitment variability, largely removing the temporal trend in δR_t . The lower CV forced the deviations to be smaller in magnitude than in the other models, but the recruitment estimates were very similar across all models. The environmental models led to a greater understanding of the system; warmer conditions had a negative impact on the recruitment of SNE–MA winter flounder. The relationship has a relatively minor impact on the estimate of the biomass of the stock, but it does provide a mechanistic link with climate to evaluate how it might respond to future conditions (Cook and Heath 2005).

Environmental relationships often break down over time (Myers 1998), and empirical management strategies that do not rely on a mechanistic environmental driver often perform better (Punt et al. 2013). Environmental relationships, however, generally persist for species at the southern extent of their range (Myers 1998), and environmental drivers could improve management strategies if there is a strong mechanistic relationship (Punt et al. 2013; Holsman et al. 2016). These tenets hold for SNE–MA winter flounder, suggesting that accounting for the environment may be important for management. While the temperature predictions from the different global earth models varied in magnitude, all models indicated an increasing trend in temperature. The particular assumptions made for this study or the exact implementation of the projections could be modified, but different implementations are unlikely to change the general trends. In the Northern Hemisphere, increasing temperature is likely to negatively impact species at the southern extent of their range (Poloczanska et al. 2013). Combining parameter estimates from an environmentally driven population model with temperature projections and fishing scenarios are a potential means for understanding stock status in the future (Hollowed et al. 2009).

With particular respect to the SNE–MA winter flounder example, however, the results are not without question. The initial increases in SSB from the projection models for a stock that is at historical lows and has had very limited fishing pressure appear optimistic. Median recruitment in the BASE run was above estimates from the population model and led to SSB that would exceed the current highest values in the time series. Temperature has historically been an important driver of recruitment in SNE–MA winter flounder (Jeffries and Johnson 1974; Keller and Klein-MacPhee 2000; Taylor and Collie 2003; Bell et al. 2014), and though median recruitment from the TEMP projection was lower than the BASE run, the impacts of temperature in the TEMP projection did not become the dominant driver until the late 2020s. Once the temperature threshold was crossed, recruitment declined, causing SSB to decrease, even in the absence of fishing pressure. The projected temperature-dependent recruitment was well above the values seen over the last 5–10 years, indicating that there are other factors that are impacting the SNE–MA winter

flounder stock that are not accounted for in this projection. Temperature is important, but it does not account for all aspects of recruitment variability (Manderson et al. 2004, 2006; Yenchow et al. 2015). Despite the problems, the TEMP run substantially deviated from the BASE run, indicating that SNE–MA winter flounder had a low probability of maintaining the rebuilding target.

The ENVIRON projection made no assumptions about the mechanistic relationship between recruitment and the environment (Brodziak et al. 1998; Punt et al. 2012; Szuwalski et al. 2015), but considered the current condition of the stock to be the best representation of the stock in the near term. Recognizing changing productivity over time and using estimates that are the most current has the potential to produce useful short-term projections. Similar to the TEMP runs, future projections with the conditions over the last 5 years suggest that the stock will not be able to attain SSB_{MSY} . While the exact estimate of biomass will vary with the explicit assumption made for the projection models (e.g., using the last 3, 5, or 10 years of data in the ENVIRON run) or the details of the ensemble of climate models, the general trend from this modelling exploration will remain the same. The reduction in recruitment due to changes in productivity, as a function of temperature or other factors, will likely make it challenging for SNE–MA winter flounder to achieve and, more importantly, sustain its biomass above the rebuilding target.

The modelling exercise conducted here is a simple example, demonstrating how external drivers in addition to fishing could impact rebuilding plans. We selected the rebuilding targets from the most recent stock assessment (NEFSC 2015). Static rebuilding targets that do not account for declines in productivity, however, may be an unfair expectation for a depleted stock (Miller et al. 2016). Reference points are a function of the stock–recruitment relationship (Quinn and Deriso 1999), and if that relationship varies with temperature, the reference points should reflect the dynamic relationship. In addition, the exercise does not contain any dynamic feedback, which is a fundamental part of fisheries management. Stocks are assessed, in some cases every year, and new regulations are implemented. In reality, poorly performing stocks would be reassessed with a focus on productivity, catch limits would be altered, and reference points could be re-evaluated. The incorporation of climate factors into population models may not dramatically alter historical abundance estimates, but are important for understanding the drivers of stock dynamics (Hollowed et al. 2013). As warmer temperature isotherms move poleward (Burrows et al. 2011), populations at the leading edge of their range are expected to increase in abundance and move into new territory, while populations at the trailing edge are predicted to decline (Beaugrand and Kirby 2010; Drinkwater 2005). Climate change and variability will affect the quantity and quality of spawning and nursery areas, prey availability, predation risk, and test the physiological constraints of species, both positively and negatively (Drinkwater et al. 2010; Hollowed et al. 2013). Along the east coast of North America, the northerly expansion of suitable thermal habitat has led to greater recruitment success and an increase in the biomass of more warm-water species such as Atlantic croaker (*Micropogonias undulatus*; Hare and Able 2007). Alternatively, cold-water species at the southern extent of their range will likely see their available habitat decrease and fragment with warmer conditions, potentially resulting in population declines (Fogarty et al. 2008; Hare et al. 2012a). With a greater understanding of the drivers of productivity, environmentally driven population models provide a tool that can move beyond projections with time-invariant parameters, which average over past conditions and incorporate factors that trend over time (Lehodey et al. 2010). For species with strong environmental influences, the coupling of population models with climate model projections (Stock et al. 2011) can provide a greater understanding of different management decisions and possibly more realistic predictions of rebuilding expectations.

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