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Original Article

Responsive harvest control rules provide inherent resilience to adverse effects of climate change and scientific uncertainty

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Climate change is altering marine ecosystem and fish stock dynamics worldwide. These effects add to scientific uncertainties that compromise fisheries management. Among the strategies that can respond to climate change and scientific uncertainty, modifications to harvest control rules (HCRs) might be among the most direct and impactful. We used a bioeconomic model to compare alternative HCRs in terms of biomass, yield, and profits in response to potential effects of climate change and scientific uncertainty, specifically simulated retrospective patterns, for 14 stocks on the Northeast Shelf of the United States. Our results suggest that a responsive HCR in which fishing mortality changes with measured changes in biomass builds inherent resilience to adverse effects of both climate change and scientific uncertainty relative to an HCR in which fishing mortality is precautionary but fixed. This was despite that fact that the HCR algorithm did not account for the climate effects modelled. A fixed fishing mortality HCR was effective when climate effects were negligible or beneficial. Scientific uncertainty further reduced biomass, yield, and profits by about the same magnitude as climate change. Our results suggest that simple changes to HCRs can be a readily implementable strategy for responding to climate change and scientific uncertainty.

Keywords: climate change, harvest control rules, New England, retrospective pattern, scientific uncertainty

Introduction

The effects of global climate change and related impacts of ocean acidification on the productivity and resilience of marine fisheries are receiving increasing attention as signals in physical, chemical, and biological metrics intensify (Sumaila *et al.*, 2011; Doney *et al.*, 2012; Pinsky and Mantua, 2014). The waters off New England in the Northeastern United States are exhibiting among the strongest climate signals in the world (Mills *et al.*, 2013), and many commercially important fish stocks in the region are vulnerable to the effects of climate change (Hare *et al.*, 2016; Kleisner *et al.*, 2017). Notably, many stocks in the iconic groundfish fishery are among the most vulnerable and remain depleted. Groundfish are especially susceptible to adverse impacts on growth, survival, and dispersal at environmentally sensitive egg and larval stages, although post-settlement life stages can also suffer adverse effects (Hare *et al.*, 2016; Klein *et al.*, 2017). The accumulated effects of these life history changes include declines in productivity and maximum sustainable yield (Fogarty *et al.*, 2008; Pershing *et al.*, 2015). Management of groundfish stocks in particular is further complicated by high levels of scientific uncertainty. Stock assessments in the region have long been plagued by retrospective patterns, which are drastic changes in estimates of biomass and fishing mortality as data from additional years are added to the model (Mohn, 1999). These retrospective patterns have generally resulted in overly optimistic perceptions of stock status in the region, leading to excessive catch limits that contribute to both overfishing and foregone yield (Wiedenmann and Jensen, 2018). In addition, scientific uncertainty might interact in further deleterious ways with climate change.

The specific effects of environmental change and scientific uncertainty on stock dynamics can be difficult to predict, yet have important implications for effective harvest strategies (Szuwalski and Hollowed, 2016). This has motivated considerable research attention focused on designing the most effective harvest strategies. Two general strategies that are often proposed in both academic research and applied policy are to use a fixed rate of fishing mortality, *F*, or to adjust *F* in response to changing conditions, which might include biomass levels or environmental variables. The chosen strategy will be a key factor shaping the harvest control rule (HCR) for a given fishery, which is arguably where science most directly meets policy in a fishery management system (Kvamsdal *et al.*, 2016). An HCR generally determines the allowable harvest from a fish stock on the basis of metrics that characterize the status of the stock. Often, this involves determining catch limits or other management measures that aim to achieve a target fishing mortality rate selected using the HCR and based on the estimated stock biomass. However, an HCR can also use other stock metrics, such as survey indices, to directly adjust quotas or effort controls, rather than linking an explicit fishing mortality rate with estimated stock biomass. Alternative HCRs could help fisheries that are currently, or might soon be, suffering adverse effects of scientific uncertainty and environmental variability to either avoid or recover more quickly from depletion. Moreover, a new HCR is a change that can often be readily implemented within an existing management framework.

When uncertainty is unbiased and variability in environmental conditions and resultant stock biomass is nondirectional, a fixed *F* HCR can be effective, especially if *F* is adjusted downward from risk-neutral reference points, such as F_{MSY} (Walters and Pearse, 1996; Restrepo and Powers, 1999; Stefansson and Rosenberg, 2005; Deroba and Bence, 2008). Reducing *F* in the face of uncertainty might be most important in avoiding biomass thresholds, below which recovery is more difficult and more restrictive management measures can be triggered (Frederick and Peterman, 1995; Roughgarden and Smith, 1996). However, adopting an HCR by which *F* responds more regularly to changes in biomass might be more effective than a fixed *F* approach in avoiding critical thresholds (NRC, 2014). When environmental variability is not simply stochastic but cyclical, the best strategy might be to select target *F*-values that track the changes in productivity, perhaps with appropriate lags (Carson *et al.*, 2009). Of course, this also increases data requirements to track the relevant cycles. Those added costs might not offset losses expected under a less data-intensive fixed *F* approach that includes a sufficient uncertainty buffer (Walters and Parma, 1996), especially if the models that incorporate environmental data are unreliable (Punt *et al.*, 2014). An intermediate approach can be to use simpler indices rather than complex and data-rich models to adjust *F* targets or quotas, although periodic modelling is still warranted to detect major changes in system state or dynamics (Parma, 2002).

Environmental variability that is not solely stochastic or cyclical but rather exhibits consistent long-term directionality might require a different approach. This is the pattern that is generally unfolding in response to climate change (Mills *et al.*, 2013), and calls for approaches for selection of target fishing mortality rates to be reconsidered (Pershing *et al.*, 2015). Even before considering appropriate forms for an HCR under directional climate-driven changes, the effects of those changes on estimation of reference points, which often determine the shape of an HCR, require careful consideration (Punt *et al.*, 2014; Szuwalski and Hollowed, 2016). Also, the implications of scientific uncertainty, especially retrospective patterns, for the performance of alternative HCRs under ongoing climate change are unclear. In fact, failure to account for time-varying parameters, which can be an effect of climate change, is often a cause of retrospective patterns in stock assessments (Hurtado-Ferro *et al.*, 2015; Szuwalski and Hollowed, 2016). Therefore, we examine the comparative performance of alternative HCRs in the face of climate change and scientific uncertainty for a series of stocks important to fisheries in the New England region.

We adopt a modified version of the modelling framework employed by Costello *et al.* (2016) and Gaines *et al.* (2018), and examine performance in terms of biomass, yield, and economic value. We selected stocks to span a range of taxonomies, life histories, management systems, and expected responses to climate change to evaluate the robustness of the outcomes. By doing so, our results provide insight into the relative effects of environmental change and scientific uncertainty on fishery performance, and whether adjustments to current HCRs are warranted.

Methods

Overview of modelling approach

We paired a Pella–Tomlinson surplus production model with an economic model to project future biomass, harvest, and profit trajectories for 14 individual stocks. We simulated effects of climate change on each stock over time by adjusting selected model parameters in each time step based on indices from the climate vulnerability assessment by Hare *et al.* (2016). Specifically, we used the results of Hare *et al.* (2016) to change the Pella–Tomlinson growth parameter, *g*, and variable fishing cost parameter, *c*, over time based on expected effects of climate change on each stock. The index is not tied to stock dynamics in a mechanistic way, and therefore our study is more useful for making relative rather than absolute comparisons among HCRs and stocks. This is consistent with the recommendation of Punt *et al.* (2014) that it is preferable to consider the performance of management strategies under plausible forecasts rather than specific predictions in the absence of reliable mechanistic models. Nevertheless, comparison with existing mechanistic models suggests that some results might underestimate expected climate effects, whereas others overestimate those effects (see Discussion section).

We parameterized the model for 14 stocks of nine species representative of many life history characteristics found in the New England and Mid-Atlantic regions of the United States (Table 1). In addition to the taxonomic and ecological diversity among these stocks, they also span a range of contemporary stock statuses, management authorities, and primary means of harvest control. We obtained biological parameters from recent stock assessments. We obtained data on prices from the US National Oceanographic and Atmospheric Administration *FishWatch* website (https://www.fishwatch.gov/) for all stocks, with the exception of Gulf of Maine cod, Georges Bank cod, and Atlantic herring, for which we used the *Fisheries of the United States* report (NOAA, 2013). We project future biomass, harvest, and profit trajectories over a 60-year time horizon for each stock. The time horizon allows 10 years for the dynamics to adjust to initial conditions, followed by 50 years to compare the performance of the HCRs thereafter. We selected this time horizon because it follows that of the assessment by Hare *et al.* (2016), on which we based the direction and magnitude of expected climate effects.

Outputs are reported as the per cent difference in each year relative to a baseline scenario that used a fixed *F* HCR without introducing climate effects or scientific uncertainty. We introduced scientific uncertainty using Monte Carlo simulations, and report the average per cent difference in each year across those

Table 1. Stocks modelled to compare the performance of HCRs, approximately ordered from the most southerly to the most northerly distributed within US waters, while grouping multiple stocks of the same species.

Common name	Scientific name	Stock	Authority	Harvest controls	Status (*B*/*F*)	Assessment
Black sea bass	*Centropristis striata*	Unit	ASMFC/MAFMC	Mixed	+/+	NEFSC (2017a)
Golden tilefish	*Lopholatilus chamaeleonticeps*	Unit	MAFMC	ITQ	+/+	NEFSC (2014a)
Striped bass	*Morone saxatilis*	Unit	ASMFC	Mixed	+/+	ASMFC (2016)
Summer flounder	*Paralichthys dentatus*	Unit	ASMFC/MAFMC	Mixed	+/−	Terceiro (2016)
Winter flounder	*Pseudopleuronectes americanus*	SNE	ASMFC/NEMFC	Mixed	−/+	NEFSC (2017b)
		GB	NEFMC	Co-op quota	+/+	NEFSC (2017b)
		GOM	ASMFC/NEFMC	Mixed	?/+	NEFSC (2017b)
Atlantic cod	*Gadus morhua*	GB	NEFMC	Co-op quota	−/−	NEFSC (2013)
		GOM	NEFMC	Co-op quota	−/−	NEFSC (2017b)
Atlantic herring	*Clupea harengus*	Unit	ASMFC/NEMFC	Fleet quota	+/+	Deroba (2015)
Atlantic sea scallop	*Placopecten magellanicus*	Unit	NEFMC	Days-at-sea	+/+	NEFSC (2014b)
American lobster	*Homarus americanus*	SNE	ASMFC	Trap limit	−/+	ASMFC (2009)
		GB	ASMFC	Trap limit	+/+	ASMFC (2009)
		GOM	ASMFC	Trap limit	+/+	ASMFC (2009)

Stock areas: Georges Bank (GB), Gulf of Maine (GOM), Southern New England (SNE), or single unit stock within US waters (unit); Management authorities: New England Fishery Management Council (NEFMC), Mid-Atlantic Fishery Management Council (MAFMC), Atlantic States Marine Fisheries Commission (ASMFC), or a combination of these bodies; Harvest controls: quota set for the entire fleet (Fleet quota), quotas allocated to harvest cooperatives (Co-op quota), individual transferable quotas (ITQ), trap limit, or combination of approaches (Mixed); Initial stock status is in terms of whether the stock is at or above the biomass, *B*, target or at or below the fishing mortality target, *F* (+), below the *B* target or above the *F* target (−), or whether either is unknown (?), at the time of the stock assessment reports used in the study, which are indicated.

simulations relative to the same baseline scenario. For more information on the base model structure and parameterization, see the Supplementary Material and Costello *et al.* (2016).

Effects of climate change on stock productivity

Hare *et al.* (2016) assigned to each species in their assessment an overall climate vulnerability score ranging from 1 to 16 based on separate sensitivity attributes and climate exposure scores. They also determined for each species the net directional effect, which indicates whether climate change is expected to affect productivity and abundance in a positive, neutral, or negative way. We combine each species' climate vulnerability score with its directional effect to generate a parameter, CC_g, which determines how much the growth parameter, g, might increase or decrease over the 60-year time horizon due to climate change. For species that received a neutral directional effect, we set $CC_g = 1$, which means that g does not change over the time horizon. For species that received a positive or negative directional effect, we calculated CC_g as follows:

$$CC_g = 1 \pm \frac{\text{VS}}{16}, \tag{1}$$

where VS is the Hare *et al.* (2016) vulnerability score, and the sign is determined by the directional score. This approach generates values ranging from 0 to 2 (Table 2), suggesting that climate change could potentially reduce growth of a species all the way to zero, or, if positive effects are expected, could double the growth rate. This range of outcomes is consistent with other estimates from the literature across a range of species.

For example, with a vulnerability score = 8 and positive directional effect, CC_g for black sea bass is 1.5. This value determines the total per cent increase or decrease in g over the time horizon. In the case of black sea bass, this amounts to a 50% increase in the growth parameter from 0.36 to 0.54 resulting from climate change between year 0 and year 60 in the model. We assume that this change accumulates in a linear manner over time, with g increasing or decreasing by the same amount every year such that the total change is achieved at the end of the time horizon. For species with multiple stocks in the region, we used the detailed species narratives provided by Hare *et al.* (2016) to determine whether vulnerability scores or directional effects different from those for the species as a whole were warranted for individual stocks. We determined that differences among stocks of American lobster were warranted, but not for other species with multiple stocks in the region (Table 2).

Effects of climate change on fishing costs

We assume that a shift in stock distribution increases costs for fishermen because vessels may need to travel farther from ports that historically relied on the stock in order maintain harvests in the short term, and over time the industry may need to adapt fishing operations and processing infrastructure to the changes (Pinsky and Fogarty, 2012; Kleisner *et al.*, 2017). This assumption is plausible, but lacks the same degree of empirical demonstration as the expected biological effects, and several mechanisms could reduce the economic impacts (see Discussion section). Hare *et al.* (2016) calculated a score representing the potential for distributional change using a subset of relevant sensitivity attributes including adult mobility, dispersal of early life stages, habitat specificity, and sensitivity to temperature. Scores are categorized as low, moderate, high, and very high. We use these scores to determine the value for a parameter, CC_c, that adjusts the costs of fishing in the model, whereby a stock categorized as having low potential for distributional change was given a CC_c score of 1, moderate potential was given a score of 1.15, high potential was given a score of 1.3, and very high potential was given a score of 1.45 (Table 2). These values are within the range of expected changes in fishing costs and catch potential for many places, and in fact might be conservative (Sumaila *et al.*, 2011; Lam *et al.*, 2016).

Table 2. Vulnerability scores, expected direction of changes, and distribution change potential from the climate vulnerability assessment by Hare *et al.* (2016), which were used to determine climate change modifiers for the Pella–Tomlinson growth parameter, CC_g, and cost parameter, CC_c.

Species	Stock	Vulnerability score	Direction	Distribution change potential	CC_g	CC_c
Black sea bass	Unit	8	+	High	1.5	1.3
Golden tilefish	Unit	9	0	Low	1.0	1.0
Striped bass	Unit	12	0	High	1.0	1.3
Summer flounder	Unit	4	0	High	1.0	1.3
Winter flounder	SNE	12	−	High	0.25	1.3
	GB	12	−	High	0.25	1.3
	GOM	12	−	High	0.25	1.3
Atlantic cod	GB	6	−	High	0.63	1.3
	GOM	6	−	High	0.63	1.3
Atlantic herring	Unit	3	−	High	0.81	1.3
Atlantic sea scallop	Unit	9	−	Moderate	0.44	1.15
American lobster	SNE	6	−	High	0.63	1.3
	GB	6	+	High	1.38	1.3
	GOM	6	+	High	1.38	1.3

Stock areas: Georges Bank (GB), Gulf of Maine (GOM), Southern New England (SNE), or single unit stock within US waters (unit). Direction of changes: positive (+), neutral (0), or negative (−).

CC_c operates in a similar way as CC_g in our model, incrementally modifying the cost parameter, *c*, in a linear way over time such that the full change is achieved in year 60. Unlike CC_g, changes introduced by CC_c are unidirectional. In other words, we assume that effects of climate change on cost will be either neutral or harmful, but will not decrease costs.

Harvest control rules

We compare the performance of a fixed *F* HCR with a responsive HCR that adjusts *F* with measured changes in biomass (Figure 1). The fixed *F* HCR optimizes the fishing mortality rate such that, when applied each year, it maximizes the net discounted future profits (i.e. net present value, NPV) in the fishery under the initial biomass and parameter values. This *F*-value is determined using an optimization routine that maximizes NPV over the modelled time horizon. For all stocks, the optimal fixed *F* is equal to 79%F_{MSY}, because the optimization function uses parameters that are common among all stocks (following Costello *et al.*, 2016; Supplementary Table S1) and reflecting negligible influence of starting conditions.

For the responsive HCR, fishing mortality in each year *t*, F_t, is a function of the biomass in that year, B_t. This function is optimized using dynamic programming to maximize NPV at each time step:

$$\max_{F1,F2\ldots} \sum_{t=1}^{\infty} \frac{\pi_t}{(1+\delta)^t}, \qquad (2)$$

where π_t is the profit in year *t* [(calculated by Supplementary Equation (S2)] and δ is the discount rate (0.05 in our study). This returns the stream of *F*-values into the future expected to maximize NPV at that time step as a function of the current B_t. To account for the US legal requirement that $F < F_{MSY}$ regardless of stock size, we constrain the maximum *F* in the responsive HCR to 90%F_{MSY}. When the model was run without climate effects included, *F* equilibrated at 70%F_{MSY} for all stocks, the same value generated by the fixed *F* optimization and used in the fixed *F* HCR.

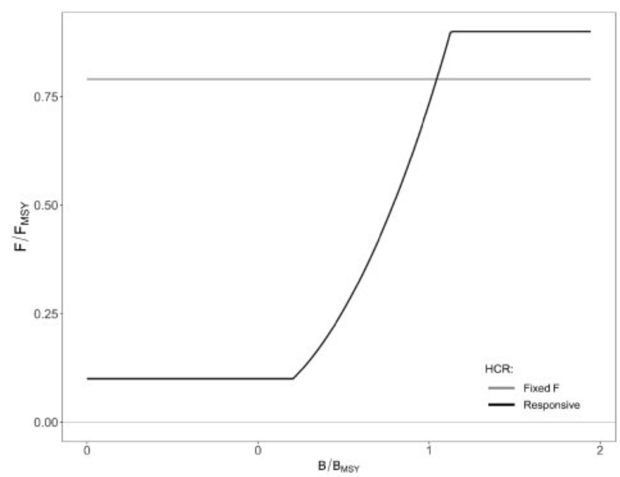

Figure 1. Examples of HCRs used in the bioeconomic model to examine performance in response to climate change and scientific uncertainty. The fixed *F* HCR uses 79%F_{MSY}, regardless of current biomass, which optimizes NPV under initial conditions, whereas the responsive HCR adjusts *F* as biomass changes to optimize NPV at each time step.

There are, of course, numerous forms that a fixed *F* or responsive HCR can take. For example, Restrepo and Powers (1999) recommend a fixed *F* HCR of 75%F_{MSY} as being effective under a wide range of biological and uncertainty characteristics. This HCR has been adopted for several stocks in the region, and is close to the optimized fixed *F* of 79%F_{MSY} used in our study. For a responsive HCR, the upper and lower bounds for *F*, the upper and lower biomass levels at which those bounds are reached, and the resulting slope of the function in between can all vary. NRC (2014) provides an illustrative HCR with an upper bound of 90%F_{MSY} at B_{MSY} and a lower bound of 10%F_{MSY} at 25%B_{MSY} (Figure 4.1c, p. 68). Our responsive HCR for Gulf of Maine cod, for example, also bounds *F* between 10%F_{MSY} and 90%F_{MSY}, but reaches the lower limit around 50% B_{MSY}, resulting in a steeper slope in between (Figure 1). Therefore, we are simulating sharper changes in F and creating contrasts that would be less pronounced with a different functional form of the responsive HCR.

Importantly, neither HCR explicitly accounted for effects of climate change by factoring in changing productivity in the calculation and optimization of NPV. A quota is determined and fully harvested in each year of the model by applying the F_t determined by the HCR in question to the biomass that year.

Scientific uncertainty

Initially, we ran the model assuming that biomass is known with certainty, and used that known biomass to determine the target fishing mortality according to the HCR in question (Figure 1), and ultimately the quota. To examine the effects of scientific uncertainty, particularly retrospective patterns, on the performance of HCRs in the face of effects of climate change, we then performed a series of Monte Carlo simulations. For each stock and HCR, we ran the model for 1000 independent iterations with scientific uncertainty in the estimation of biomass. Scientific uncertainty was simulated by multiplying the actual biomass at each time step by a random variate to generate the estimated biomass. This affected selection of the target F_t determined by the responsive HCR, but not by the fixed F HCR, for which F_t does not change with estimated biomass. For both HCRs, measurement error affected the calculation of quotas by substituting the estimated biomass as modified by the random variate for the actual biomass in each year, which simulates implementation error due to scientific uncertainty.

Random variates were drawn from a log-normal distribution with a mean of 1.2 and a standard deviation of 0.1, which simulates retrospective patterns that produce overestimates of biomass (Supplementary Figure S1). Some stock assessments in the regions exhibit relatively small retrospective patterns, whereas groundfish assessments can exhibit much stronger patterns (Wiedenmann and Jensen, 2018). Therefore, our simulated error is excessive relative to recent assessments for some stocks while underestimating uncertainty for others, with the objective being a common error rate that is plausible and enable comparisons among stocks. We do not consider retrospective patterns that result in underestimates of biomass because these are rare in the region, but these errors might interact with climate effects in different ways. The same 1000 series of 60 random variates were used in the replicate simulations for each HCR to allow the outcomes to be more directly comparable.

Results

Performance of HCRs in response to climate change

Trajectories of biomass (Figure 2), harvest (Figure 3), and profits (Figure 4) were generally unidirectional with consistent rates of change under the fixed F HCR. These trajectories were steadily downward for stocks expected to suffer the most adverse effects of climate change, flat for stocks expected to experience more modest effects, and upward for stocks expected to benefit (Table 2; Figures 2–4).

In contrast, trajectories were more complex under the responsive HCR, mostly reflecting some sensitivity to initial conditions. For stocks estimated to be at high relative biomass at the start of the time series, biomass initially declined (Figure 2a, g, j, k, m, and n). Higher yields could be extracted profitably from these abundant stocks, although harvest and profits then declined for a short period following an initial "windfall" as biomass approached the economic optimization level (Figures 3a, g, j, k, m, and n and 4a, g, j, k, m, and n). However, for stocks that began at lower relative biomass, biomass initially climbed as recovery progressed (Figure 2b–f, h, i, and l), with associated increases in harvest (Figure 3b–f, h, i, and l) and profits (Figure 4b–f, h, i, and l). Following these initial adjustments, trajectories of all metrics for all stocks followed expected effects of climate change, similar to the trends for the fixed F HCR (Table 2; Figures 2–4).

Despite the similar trends between the fixed F and responsive HCRs, there were noticeable differences in the magnitude of the responses, at least for those stocks expected to either benefit or suffer from effects of climate change. For stocks expected to experience modest effects of climate change, the two HCRs performed comparably across all metrics (Figures 2b–d, 3b–d, and 4b–d). For those stocks expected to benefit from effects of climate change, the fixed F HCR maintained higher relative biomass over time (Figure 2a, m, and n). However, this does not necessarily reflect poor performance of the responsive HCR. Given that the fixed F HCR involves fishing at only a fraction of F_{MSY} (Figure 1), biomass by design is maintained at a conservative level. Furthermore, harvest and profits were both higher over time for the stocks expected to benefit from effects of climate change under the responsive HCR, so maintaining higher biomass came at a cost of yield and profits (Figures 3a, m, and n and 4a, m, and n). The differences between the HCRs were greater for harvest, with only modest differences in profits, so the fixed F HCR produced something akin to Hilborn's (2010) "pretty good yield," at least from an economic perspective.

For those stocks expected to experience adverse effects of climate change, the responsive HCR generally outperformed the fixed F HCR in terms of biomass conservation (Figure 2e–i, k, and l), with the exception of Atlantic herring (Figure 2j). Differences in yield and profits, however, were generally modest over most of the time series for all of these stocks (Figures 3e–l and 4e–l). Atlantic herring is a stock that is not expected to be affected by climate change as adversely as others (Table 2) and is estimated to have very high biomass at the start of the time series. The responsive HCR resulted in a steep initial reduction in herring biomass to maximize yield and profits (Figures 3j and 4j), after which subsequent changes were negligible. In contrast, the fixed F HCR resulted in a steady decrease in biomass over time, converging with the trend for the responsive HCR near the end of the time series.

Performance of HCRs with scientific uncertainty

When scientific uncertainty was added to the model, similar trends and relative differences among the HCRs were generally maintained, but with some notable exceptions. For stocks expected to experience modest effects of climate change, and for which all metrics showed generally flat trends, the fixed F HCR performed much better than the responsive HCR with scientific uncertainty, especially in terms of biomass (Figure 2b–d). This contrasted the similar performance of the HCRs in the absence of scientific uncertainty. In fact, for these stocks, the fixed F HCR with scientific uncertainty performed about as well as the responsive HCR did without scientific uncertainty. This was likely due to the fact that scientific uncertainty was biased towards overestimation of biomass, which would result in selection of

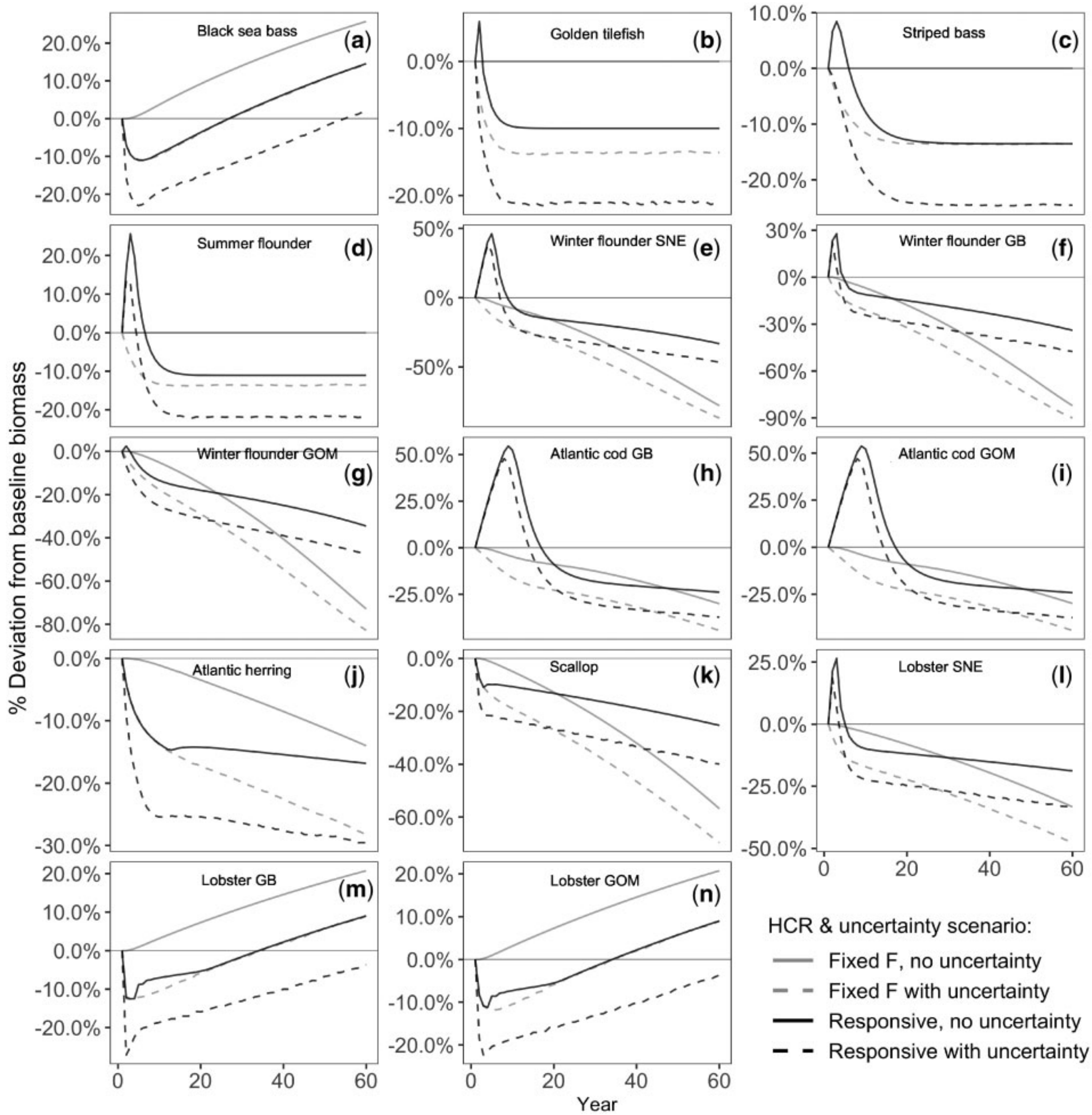

Figure 2. Comparative performance of the fixed *F* HCR and responsive HCR in terms of stock biomass conservation in response to potential effects of climate change and scientific uncertainty on 14 stocks in the Northeastern United States. Results are percentage deviations in each year of the model from a baseline scenario that used a fixed *F* HCR without effects of climate change or scientific uncertainty. Stock areas include Georges Bank (GB), Gulf of Maine (GOM), and Southern New England (SNE). Others are managed as a single unit stock within US waters. Note that axis scales differ among plots due to differences in the magnitude and direction of results.

higher *F* than warranted under the responsive HCR, but not the fixed *F* HCR.

For stocks expected to benefit from effects of climate change, the same patterns were evident when scientific uncertainty was added as were evident in its absence. The fixed *F* HCR maintained higher biomass (Figure 2a, m, and n), but the responsive HCR maintained higher yield and profits (Figures 3a, m, and n and 5a, m, and n), with all metrics increasing through time. However, the magnitude of each metric for a given HCR was lower with scientific uncertainty added, and the differences between the two HCRs became smaller.

Conversely, for stocks expected to suffer adverse effects of climate change, biomass losses were reduced by the responsive HCR with scientific uncertainty, and in many cases were less than those experienced under the fixed *F* HCR in the absence of scientific uncertainty (Figure 2e–i, k, and l). This suggests that the risks of overestimating biomass and setting *F* too high as a result of the biased error structure were, over time, outweighed by the benefits of tracking long-term declines in productivity. Atlantic herring was again an exception to this pattern (Figure 2j). Similar to the results for stocks expected to benefit from effects of climate change, differences in yield and profits were minor over most of

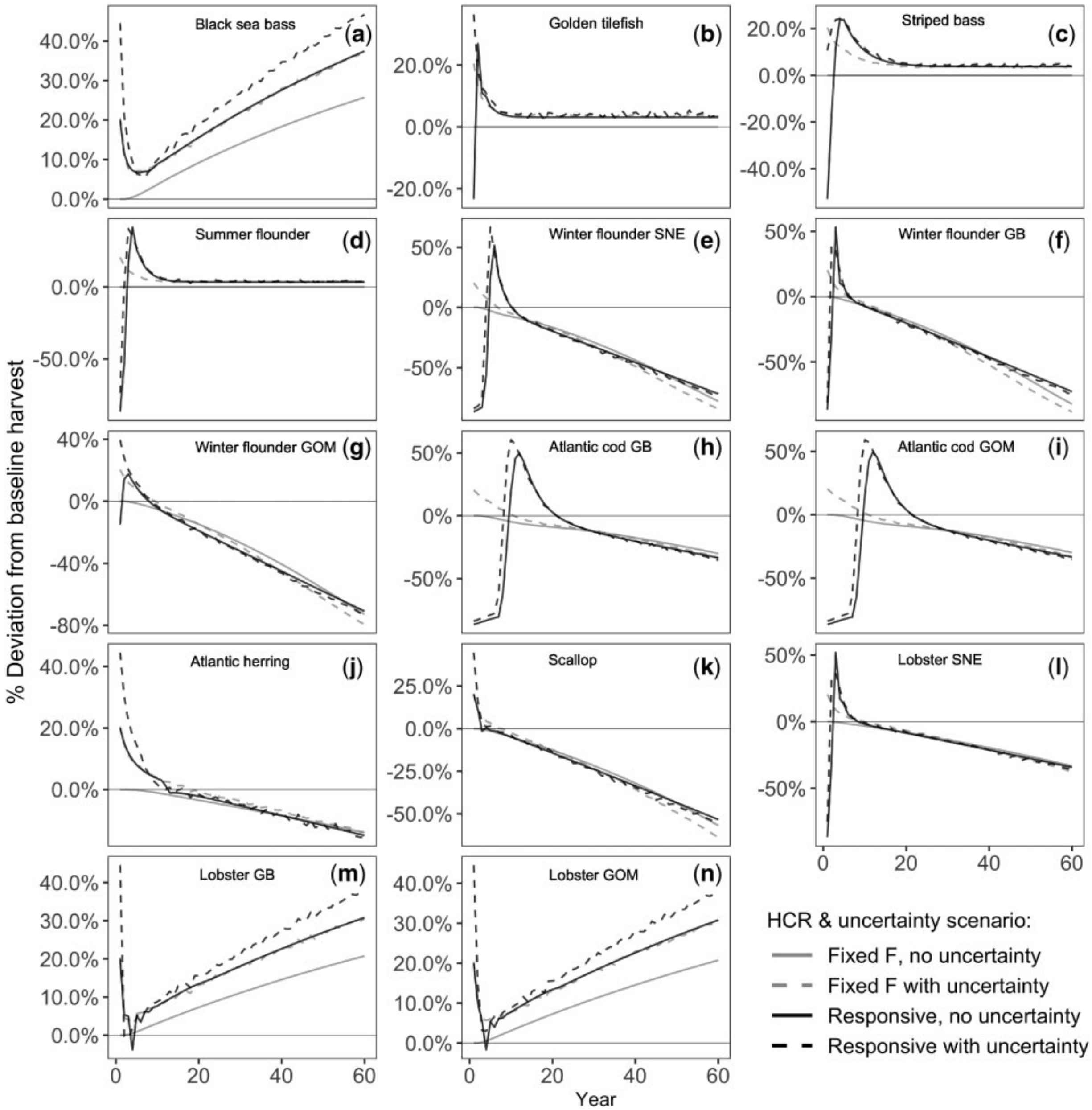

Figure 3. Comparative performance of the fixed *F* HCR and responsive HCR in terms of fishery yield in response to potential effects of climate change and scientific uncertainty on 14 stocks in the Northeastern United States. Results are percentage deviations in each year of the model from a baseline scenario that used a fixed *F* HCR without effects of climate change or scientific uncertainty. Stock areas include Georges Bank (GB), Gulf of Maine (GOM), and Southern New England (SNE). Others are managed as a single unit stock within US waters. Note that axis scales differ among plots due to differences in the magnitude and direction of results.

the time series for the other stocks likely to suffer adverse effects of climate change, with some larger difference emerging towards the end (Figures 3e–i, k, and l and 4e–i, k, and l).

Discussion

Responsive HCRs as a resilience strategy

Our most important finding is that an HCR that makes more regular and often incremental changes in *F* as changes in biomass are detected generally reduced the expected adverse effects of both climate change and scientific uncertainty relative to a fixed *F* approach. An HCR that is responsive to changes in biomass can therefore be a resilience strategy that is low-cost and easy to implement, even if the function itself is fixed through time. Notably, the form of our responsive HCR aimed to maximize profits rather than achieve a biomass conservation objective, and did not explicitly account for effects of climate change. A responsive HCR structured to achieve dual objectives would likely have achieved stronger biomass outcomes, and sooner, albeit possibly at some cost in yield or profits. A responsive HCR structured to account for climate effects would likely have performed better, but in practice would incur costs that offset its benefits to some degree

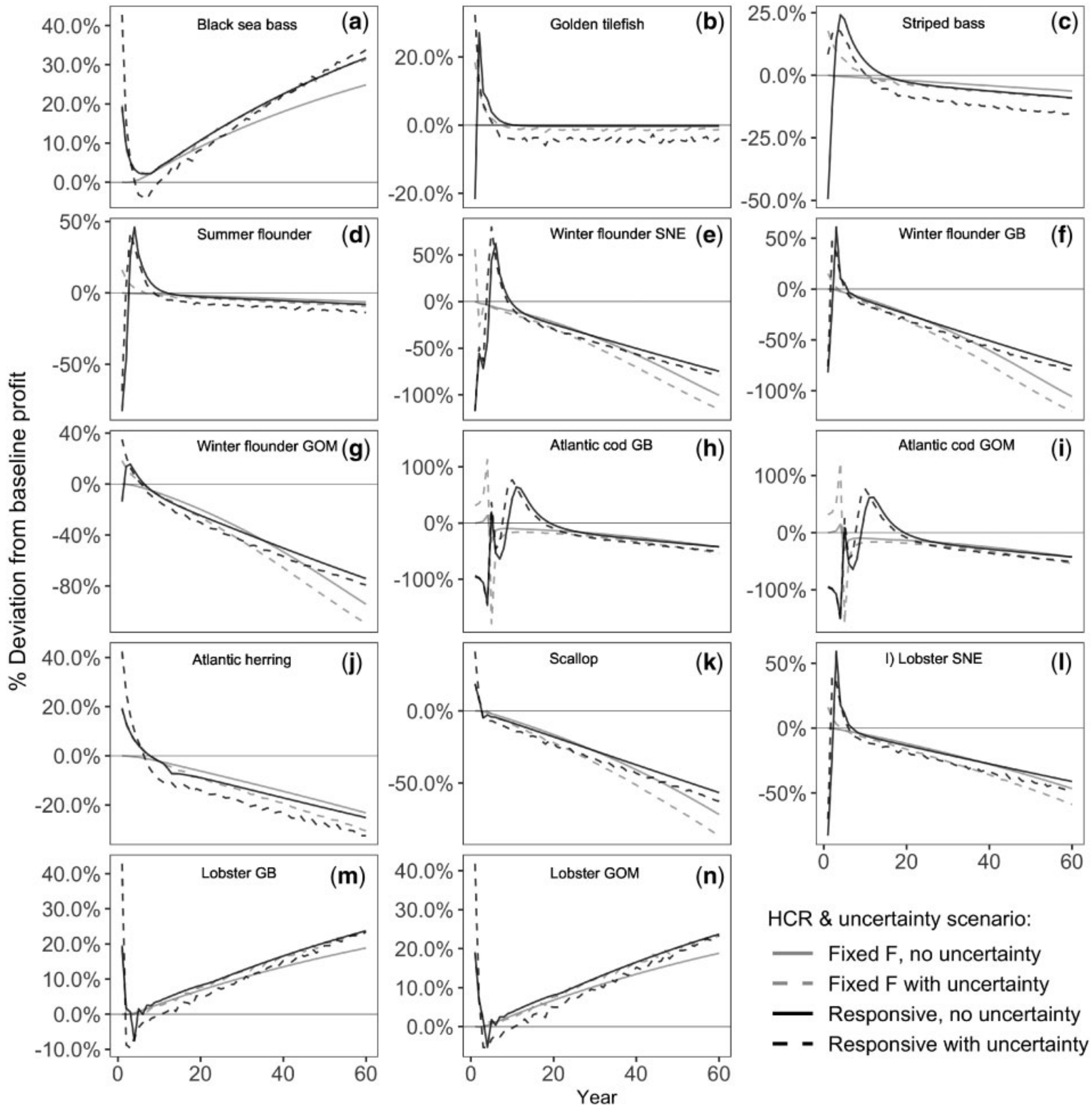

Figure 4. Comparative performance of the fixed *F* HCR and responsive HCR in terms of expected net future profits in response to potential effects of climate change and scientific uncertainty on 14 stocks in the Northeastern United States. Results are percentage deviations in each year of the model from a baseline scenario that used a fixed *F* HCR without effects of climate change or scientific uncertainty. Stock areas include Georges Bank (GB), Gulf of Maine (GOM), and Southern New England (SNE). Others are managed as a single unit stock within US waters. Note that axis scales differ among plots due to differences in the magnitude and direction of results.

(Walters and Parma, 1996). Selecting the best underlying function for a responsive HCR in the face of direction climate-driven change and scientific uncertainty should be based on management strategy evaluation (Punt *et al.*, 2014), but our results suggest that fishery performance will improve through the more fundamental shift from a fixed *F* approach to one in which *F* varies as conditions change. The benefits of responsive HCRs have been articulated and demonstrated in multiple studies, especially with respect to avoiding and recovering from severe stock depletion (reviewed by NRC, 2014). However, those studies do not consider the directional and often adverse effects of climate change on fish stocks. Our study therefore provides an additional argument in support of these approaches.

Do these results imply that scientists and managers can simply ignore effects of climate change by adopting a responsive HCR? Like any model, ours includes important assumptions that might make the outcomes stronger than would be seen in practice (alongside other assumptions that might make the results fairly conservative; see below). Furthermore, an HCR only addresses one objective: establishing appropriate *F* targets. Although this is arguably the most important aspect of fishery management (Liu *et al.*, 2016), other issues are also important and in need of attention. For example, preserving complex spatial structure of fish populations often requires a dedicated suite of scientific and management approaches (Kritzer and Liu, 2014), as does protection and restoration of critical habitats (Kritzer *et al.*, 2016). Spatial structure and habitat are susceptible to effects of climate change (Kleisner *et al.*, 2017; Smith *et al.*, 2017), yet are rarely incorporated into stock assessments and are not effectively addressed by stock-wide *F* targets (Caddy, 2014; Kerr *et al.*, 2017). Attending to these issues, including expected climate effects, promotes the needed evolution towards ecosystem-based approaches in fisheries management in New England (O'Boyle *et al.*, 2012) and worldwide (Pikitch *et al.*, 2004).

For those stocks expected to experience modest or positive effects of climate change, the fixed *F* HCR generally performed as well or better than the responsive HCR, especially when scientific uncertainty was added to the model. However, the majority of stocks in the waters off New England are expected to experience adverse effects of climate change (Hare *et al.*, 2016), so fixed *F* HCRs should arguably be the exception rather than the rule in this region and others experiencing similarly adverse effects of climate change. Moreover, continued efforts to reduce scientific uncertainty will certainly improve performance of responsive HCRs, since uncertainty affects these HCRs in both selecting the target *F* and calculating the quota, vs. only affecting quota-setting with a fixed *F* HCR. It will be important to determine, however, that the benefits realized from reducing uncertainty outweigh the costs, else a simpler HCR that is robust to the uncertainty might be preferable (Walters and Parma, 1996).

Confronting scientific uncertainty

It is notable that adding scientific uncertainty to the model led to additional reductions in biomass for many stocks on the order of those experienced due to climate effects alone. This underscores the importance of continued efforts to better understand stock dynamics, whether climate change is having strong effects or not. We included a common error structure for all of the stocks in our study, but in practice it will look very different among stocks. For instance, whereas retrospective patterns plague groundfish assessments in the region (Wiedenmann and Jensen, 2018), the sea scallop stock assessment employs multiple models that often corroborate one another and build greater confidence in the underlying science (NEFSC, 2014b). There are many reasons for the contrasting levels of uncertainty between the sea scallop and groundfish fisheries: single-species vs. multispecies fishery, sessile vs. mobile organisms, single gear vs. multi-gear fleet, newer fishery vs. the oldest commercial fishery in the nation, and so on. Regardless of the causes, science, and management of each fishery must respond to very different uncertainty profiles.

Still, uncertainty will always be a factor in management of any complex ecological system. Therefore, equally important is developing clear risk tolerance policies, and adopting management strategies that are appropriately risk-averse in response (Sethi, 2010). In some cases, significant precaution against overfishing will be warranted, such as when the stock has high ecological, economic, or cultural value. Precaution generally means foregoing some potential yield in the near-term to increase the probability of maintaining stable biomass and yield over a longer term. Weighing that trade-off is a policy question that should be informed by science, including biology, ecology, economics, and other social sciences.

For example, the Atlantic herring fishery targets an abundant forage fish that serves as prey for a wide range of predators, supports a large fleet spread across many ports in the region, and supplies the primary source of bait to the lucrative American lobster fishery, that itself supports an even larger fleet. Therefore, overfishing the herring stock could have severe social, economic, and ecological consequences that reach well beyond the fishery, and, thus, more conservative management may be warranted. The fishery is currently considering alternative HCRs to balance this complex suite of issues (Deroba *et al.*, 2018). In contrast, the golden tilefish fishery targets a species with fewer trophic connections, supports a very small fleet, and has lower second-order importance for other industries. Therefore, more risk-prone approaches could be justifiable in management of the fishery, depending on the risk tolerance of the participants. Despite these differences, our model used common HCR algorithms for all stocks, whereas in practice different percentages of F_{MSY} might be needed for fixed *F* HCRs, and different objective functions might be needed for responsive HCRs, based on the risk profile of the fishery in question. However, this does not negate the generally greater effectiveness of responsive HCRs in the face adverse effects of climate effects and scientific uncertainty.

Implications of model assumptions

By design, our study aimed to compare directional changes and relative differences, but not to predict absolute changes. The vulnerability assessment by Hare *et al.* (2016) provided an effective vehicle for aggregating a wide range of climate-related impacts in a consistent manner across the focal stocks that is well-grounded in our current stage of knowledge. However, one critical assumption is that the impacts will accumulate in an incremental and linear manner. Nonlinearities, especially sharp discontinuities such as those associated with regime shifts or tipping points (Pershing *et al.*, 2014; Selkoe *et al.*, 2015), could change our most important conclusions. It is unlikely that effects of those types would make a fixed *F* HCR perform better than a responsive HCR as stocks suffer effects of environmental change, however. Rather, sudden and pronounced changes in stock or ecosystem dynamics are more likely to overwhelm the performance of any HCR policy, and fundamentally change many dimensions of fishery management, including the primary species being targeted and managed. Of course, if a new system state takes effect, our findings are likely to be applicable within that new context as it evolves. Moreover, there is ample evidence that more regular and incremental changes as assumed in our study are unfolding in many contexts (Walsh *et al.*, 2015; Tommasi *et al.*, 2017), and our approach is therefore relevant in those cases.

We also assumed that shifting stock distributions will introduce progressively higher costs for ports and fleets that have historically depended on those stocks. This assumption does not account for potential adaptations by fishing fleets, such as employing new gears or landing in new ports, or the possibility that new fleets and ports will come to focus on stocks that become more prevalent in their areas as stocks shift their geographic distribution. Although these changes would reduce the costs of climate change from those we projected, we conjecture that costs would still increase, at least for some time as the system adjusts, so the assumption remains reasonable. Notably, several fisheries in our study utilize rights-based management models whereby quota is allocated to individuals or cooperatives. These approaches can facilitate transfer of access to stocks by short-term leasing or longer-term transfer of quota among industry members more rapidly than is often possible through governance authorities. Therefore, rights-based management could provide inherent resilience to climate change, even if that is not an explicit objective of programme design, similar to the inherent benefits of responsive HCRs that we illustrate. This hypothesis warrants research attention.

We modelled climate-driven changes unfolding over a 60-year time horizon, resulting in biomass declines of 50% or more for some stocks under some HCRs. By comparison, Pershing *et al.* (2015) predict changes of a similar magnitude for Atlantic cod, but realized much more quickly. Similarly, Hare *et al.* (2010) estimated changes in productivity of a species expected to benefit from climate change in the region, the Atlantic croaker, on the order of the changes in our model for the sympatric and ecologically similar black sea bass. Therefore, although we aimed to discern relative differences, the absolute changes modelled might be reasonable approximations for some stocks. We also relied on Hare *et al.* (2016) for the directionality of the effects of climate change on fish stock growth, but even this is debatable in at least one case. Hare *et al.* (2016), and therefore our study, project that the American lobster stock in the Gulf of Maine will improve growth as a consequence of climate change. In contrast, Le Bris *et al.* (2018) recently predicted a long-term decline in productivity of American lobster in the Gulf of Maine, resulting in a decrease in abundance of lobsters on the order of 40% over 35 years, highlighting the importance of future work on this important variable.

With respect to the scientific and management processes, we assumed that stocks are assessed and quotas set every year in the model, but that the underlying HCR does not change through time. In practice, this is rarely the case in New England fisheries. However, and with only a few exceptions such as the sea scallop fishery, stock assessments are generally conducted every 2–5 years, with quotas then set for the intervening years until the next assessment. This allows the consequences of inaccurate biomass estimation, often due to retrospective patterns, to be compounded, which heightens the importance of responding to biomass declines when they are detected by reducing fishing mortality.

However, HCRs as applied in practice can vary through time. For example, the New England groundfish HCR specifies $75\%F_{MSY}$ as the default basis for setting catch limits, and also permits scientific advisors to deviate from that default in response to particular circumstances based on their expert judgement (Department of Commerce, 2010). *Ad hoc* deviations from the default HCR have been common, and HCRs for some stocks have changed from *F*-based approaches to changes in quota based on survey indices (*sensu* Parma, 2002). Nevertheless, $75\%F_{MSY}$, which is close to the $79\%F_{MSY}$ used in our optimized fixed *F* HCR, has still been the most frequently used basis for catch limits in the region, chosen explicitly in response to awareness of scientific uncertainty, although arguably without full appreciation of its magnitude. In contrast, the structure and application of the responsive HCR in our model assume perfect information. Had we incorporated awareness of scientific uncertainty into the structure or application of the HCR, the relative differences from the fixed *F* HCR might have differed, although the likely direction and magnitude of those changes are unclear.

Finally, the magnitude of retrospective patterns seen in some stock assessments suggests that the error distribution we used is conservative, and we might have seen even stronger differences had we simulated larger errors. Also, retrospective patterns are only one type of scientific uncertainty, and there are additional uncertainties in the ability of management measures to meet fishing mortality targets (e.g. due to limited monitoring of catch). Including additional uncertainties might have further exacerbated differences among HCRs, or reduced differences, depending on the nature of the uncertainties and their effects.

Conclusions

Climate change is adding to the already considerable complexities and uncertainties inherent in fisheries science and management, and promises to change the productivity of many fish stocks. Addressing this impact is daunting, and far from straightforward. Tracking productivity change is a difficult task, and is often done using analysis of historical data. This could mean identifying productivity change well after it has occurred. If productivity has declined, but has not yet been detected, this may mean that catch limits are set at levels that unknowingly result in overfishing, which could have long-term adverse effects on fisheries. Our analysis suggests that those adverse effects could be avoided, or at least reduced, by applying HCRs that respond to changes in biomass. Biomass fluctuations are much easier to track than changes in productivity. HCRs that become more precautionary as biomass declines can inherently respond to productivity change, even if that change is undetected. This reduces the likelihood of overfishing, and improves our ability to cope with climate-related uncertainties in fishery management.

The importance of sustainable management of marine fisheries for maintaining livelihoods, food security, cultural heritage, and ecosystem health compels us to confront the challenges posed by climate change, especially given that it will progress for some time whether meaningful mitigation steps are taken or not. Adoption of ecosystem-based management approaches that attend to habitat, species interactions, and other ecosystem components and processes has the potential to increase productivity and resilience even as climate changes causes many adverse effects. However, design, implementation, and evolution of those management systems takes time, as will realizing the expected benefits. Our study suggests that a simple step that can be readily implemented—use of responsive HCRs that make regular adjustments to fishing mortality as changes in biomass are detected—can provide inherent resilience and begin to reduce the adverse effects of climate change on many stocks while more complex solutions are added to further address those impacts.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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