A framework for modelling fish and shellfish responses to future climate change

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A framework is outlined for a unified approach to forecasting the implications of climate change on production of marine fish. The framework involves five steps: (i) identification of mechanisms underlying the reproductive success, growth, and distribution of major fish and shellfish populations, (ii) assessment of the feasibility of downscaling implications of climate scenarios derived from Intergovernmental Panel on Climate Change (IPCC) models for regional ecosystems to select and estimate relevant environmental variables, (iii) evaluation of climate model scenarios and select IPCC models that appear to provide valid representations of forcing for the region of study, (iv) extraction of environmental variables from climate scenarios and incorporation into projection models for fish and shellfish, and (v) evaluation of the mean, variance, and trend in fish and shellfish production under a changing ecosystem. This framework was applied to forecast summer sea surface temperature in the Bering Sea from 2001 to 2050. The mean summer surface temperature was predicted to increase by 2°C by 2050. The forecasting framework was also used to estimate the effects of climate change on production of northern rock sole (*Lepidopsetta polyxystra*) through projected changes in cross-shelf transport of larvae in the Bering Sea. Results suggest that climate change will lead to a modest increase in the production of strong year classes of northern rock sole.

Keywords: climate change, fish and shellfish management, fisheries oceanography, spawner–recruitment, stock projection models.

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Introduction

The recent report of the Intergovernmental Panel on Climate Change (IPCC) concludes that "There is very high confidence that the global average net effect of human activities since 1750 has been one of warming" (http://www.ipcc.ch/graphics/gr-ar4-wg1.htm; IPCC, 2007). These changes in climate, in concert with associated environmental disturbances and other drivers, are expected to have lasting effects on the properties of marine ecosystems and the goods and services extracted from them. With a few exceptions, the IPCC AR4 assessment provides qualitative rather than quantitative predictions of effects on marine resources (Fischlin *et al*., 2007). The report identifies several sources of uncertainty that contributed to the reliance on qualitative statements, including inadequate representation of the interactive coupling between ecosystems and the climate system, such as limitations of climate envelope models used to project responses of individual species to climate change, interactions between climate change, and changes in human use and management of ecosystems. Since the publication of the report, analysts have endeavoured to evaluate the climate–ecosystem couplings (Di Lorenzo *et al*., 2008) and new techniques for selecting climate scenarios for use in projections (Overland and Wang, 2007; Wang *et al*., in press). This paper presents a framework to use these new results to make quantitative forecasts of climate-change effects on fish and shellfish that can be used as part of a coordinated global effort to assess these effects on commercial fish and their fisheries throughout the world's oceans.

Since the publication of the IPCC AR4 report, scientists around the world have formed interdisciplinary research teams to improve our understanding of the linkages between climate forcing on marine ecosystems and the response of marine fish and shellfish (Brander, 2008; Hollowed *et al*., 2008; ICES, 2008). These groups are exploring techniques for quantifying the effects of climate change on the reproductive success, growth, and distribution of marine fish and shellfish. ICES and PICES sought to facilitate these global research efforts by forming a joint

ICES/PICES Working Group that would promote the development of quantitative forecasts of climate effects on fish and shellfish in the world's oceans (http://www.ices.dk/workinggroups/ViewWorkingGroup.aspx?ID=331).

Three modelling approaches are typically applied to evaluate the effects of climate change on fish and shellfish resources.

(i) Statistical downscaling: regional scenarios are estimated from IPCC model projections and are used to forecast time-series of regional environmental variables (e.g. monthly temperature, advection, prey availability, predator abundance, and habitat volume) that are incorporated into stock projection models to estimate future fish or shellfish production.

(ii) Dynamic downscaling on regional scales: IPCC model output is coupled to regional ocean models to project changes in nutrients, phytoplankton, zooplankton, and higher trophic level responses and feedbacks.

(iii) Dynamic global models: fully coupled biophysical models at the global scale that operate at time and space scales relevant to coastal domains.

It is likely that all three modelling approaches will draw on information derived from correlative, mechanistic, and analogue studies (Fischlin *et al.*, 2007). Extensions of these modelling approaches could include simulations to evaluate the performance of different management strategies under changing ocean conditions (A'mar *et al.*, 2009).

There are trade-offs between all three modelling approaches. From a physical perspective, statistical downscaling requires that each of the local environmental variables can be linked to the climate or regional forcing that can be projected by the IPCC global climate models (GCMs). Often, the functional relationships between the local environmental conditions and the climate or regional forcing have not been determined or they are uncertain. From a biological perspective, developing forecasts based on environmental variables may not perform well, because the responses of fish and shellfish to changes in environmental conditions are represented by simplified interactions that may miss non-linear responses or feedbacks within the system (Hsieh *et al.*, 2005; Steele, in press). However, complex biophysical models may suffer from a lack of information on key parameters and a high likelihood of model misspecification. The trade-offs between modelling approaches, and the knowledge that the results will be used to form high stakes management decisions, suggest that multiple modelling approaches should be considered and skill assessments should be regularly performed to inform the public on the inherent uncertainties associated with the projections (Stow *et al.*, 2009).

We recognize that reliable biological projections necessitate getting the climate forcing correct. In this regard, current models have demonstrated the ability to simulate the past few decades of the mean climate reasonably well (Reichler and Kim, 2008), and presumably, this applies to their 21st century forecasts as well. Owing to the chaotic nature of the climate system, it is impossible to forecast the timing and phases of future oscillations in the climate system. Although specific forecasts are therefore not feasible, the models do appear suitable to explore the probable changes in the overall properties of the climate forcing.

The global need for baseline quantitative information on potential climate-change effects on fish and shellfish warrants a two-pronged approach. Rapid progress can be made using statistical downscaling where environmental variables are projected and incorporated into existing stock projection models using existing knowledge of mechanisms linking fish and shellfish response to biophysical forcing. Time-series generated for this effort can be used in retrospective analyses to evaluate the performance of models and validation of hypothesized functional relationships. In parallel, the longer term, and more costly, effort involved in developing sufficient understanding to implement dynamic downscaling by developing coupled biophysical models should be commenced as a means of addressing complex feedbacks in marine ecosystems. This paper describes a framework for making the first type of forecast.

Methods

The proposed statistical framework involves the following steps:

(i) identification of mechanisms that explain environmental influences on the reproductive success, growth, and/or distribution of major fish and shellfish populations;

(ii) identification of the key environmental variables needed to model fish and shellfish responses to environmental variability;

(iii) assessment of the feasibility of using IPCC model-simulation results to predict environmental variables;

(iv) comparison of IPCC model hindcasts with observed 20th century conditions on a regional basis, to select and weigh the IPCC model scenarios, to develop an ensemble for use in projections;

(v) estimation of environmental variables using the ensemble projection and incorporation of time-series of environmental variables into stock projection model(s) for fish and shellfish;

(vi) evaluation of the effects of harvest strategy under changing ecosystem conditions.

Methods for selecting environmental variables

In most regions, fisheries oceanographers have conducted retrospective and process studies designed to improve our understanding of the processes linking ecosystem forcing to reproductive success, growth, and distribution of commercial species (for recent examples, see papers included in symposium volumes described by Daan and Fogarty, 2000; Fogarty, 2001; Royer and Dagg, 2002; and Batchelder *et al.*, 2005). These fisheries-oceanography programmes provide a basis for selection of environmental variables to use in predicting climate-change effects on commercial fish and fisheries.

Once the environmental variables have been identified, fisheries oceanographers and climate scientists should meet to explore the feasibility of extracting variables from IPCC model projections. This step often requires an exploration of techniques to connect the climate forcing to the environmental factors at the spatial and temporal scales relevant to fish and fisheries. The newly formed ICES/PICES Working Group on Forecasting Climate Change Impacts on Fish and Shellfish facilitates this type of communication and scientific exchange.

Methods for projecting environmental variables

There is a variety of ways to formulate future climate scenarios based on the results of IPCC models (Tebaldi *et al.*, 2005).

In general, it is prudent to consider the output from multiple models because of the uncertainties inherent in any individual climate projection. These uncertainties arise because the models are imperfect and because of the intrinsic variability of the climate system. In other words, from a single simulation, it can be very difficult to separate a meaningful signal from the climate "noise" that exists over a vast range of time-scales. One approach is to apply a quasi-Bayesian method to construct weighted ensemble mean projections of regional environmental conditions. This method is based on the understanding that different models have different strengths and weaknesses, and that the better models for a particular parameter in a particular region should be given greater consideration. Our procedure represents an adaptation of the method developed by Raftery *et al.* (2005) for combining the results from numerical weather-prediction models for short-term weather forecasts, and is outlined below.

The various IPCC model outputs are evaluated and rated, based on the fidelity of their hindcasts for the latter half of the 20th century, in terms of replicating observed conditions. The errors in these hindcasts are computed for individual parameters and for specific regions. Multiple criteria are considered for each parameter, including replication of the means, as well as modelled vs. observed variances and potentially additional measures, such as trends and seasonality. The errors are then used to construct "distances" between the model and observations for each model simulation. The distances form the basis for assigning weights for each model using the following expression $W_i = \exp(-D_i/D_m)$, where W_i is the weight for the individual model run i, D_i the individual model distance error, and D_m the mean of the model error distances. The ensemble weighted mean projections are then given by $F_{\mathrm{ens}}(t) = \sum_{i=1}^{n} W_i \times F_i$, where $F_i(t)$ are the bias-corrected model projections at time t. The weights, W_i, are also used to compute the variance/uncertainty in the model projections incorporating both intermodel and intramodel forecast variability. As pointed out by Raftery *et al.* (2005) among others, the Bayesian approach has many optimal properties from a statistical perspective.

An example of the selection method

We provide an example of the technique described above using summer sea surface temperature (SST) over the Bering Sea shelf as the parameter of interest. This parameter represents an important aspect of the oceanography, and is associated not just with the suitability of the habitat for temperature-sensitive species, but is also related to the stratification, and hence the vertical mixing of nutrients into the euphotic zone and ultimately primary production (Hunt *et al.*, 2002).

Evaluation of the 20th century model hindcasts was carried out for the region extending from 55°N to 65°N and 165°W to 175°W for the average SST for July–September. This evaluation was restricted to the subset of models found to replicate the essential character of the Pacific Decadal Oscillation (PDO; Mantua *et al.*, 1997). The PDO represents the leading mode of variability in SST in the North Pacific, and can be considered an "acid test" of a model's ability to account for the atmospheric variability, oceanic circulation, and air–sea coupling in the North Pacific. The models that passed the PDO test (Overland and Wang, 2007) were evaluated with respect to their simulations of the mean, interannual variance, and average trend (1948–2007) in seasonally averaged SST over the shelf (Figure 1). The validating dataset was obtained from the NCEP Reanalysis (Kistler *et al.*, 2001).

The weights applied to the models, based on the accuracy of their hindcasts in terms of reproducing the mean, variance, and trend in the observed SST of the Bering Sea shelf over the last half of the 20th century, described above, are illustrated in Figure 2 (The normalized errors that these weights are based on range from about 0.5 to 10.). The highest and second-highest rated models were the high-resolution Canadian model (CCCMAT-63) and the medium-resolution Japanese model (MIROC-med), respectively. The two lowest rankings were the two US Geophysical Fluid Dynamics Laboratory (GFDL) models, GFDL2.0 and GFDL2.1. The latter models included sizable errors in their hindcasts of both the mean and the trend in SST (they indicated substantial cooling over the latter half of the 20th century). It seems reasonable that the contributions of these two models to the ensemble mean, even with bias-correction, received little weight.

A time-series of SST for the first half of the 21st century, based on an ensemble-weighted mean, is displayed in Figure 3. This projection was based on the model simulations incorporating the middle-of-the-road A1B emission scenario. The results of the IPCC simulations vary little with the assumed emission scenario for the first half of the 21st century. Much more dramatic differences among the various scenarios are simulated for the second half of the 21st century, which represents another source of uncertainty. The ensemble results for the late summer SST on the Bering Sea shelf featured a near constant warming trend of ~0.4°C per decade. Note that the ensemble mean effectively averaged out most of the year-to-year variability that exists in the individual model simulations. The Bayesian method indicated an expected standard deviation of ~1°C (as illustrated by the vertical bars in Figure 3) about the ensemble mean in any particular year, with a small increase over time in this uncertainty over the 2000–2050 period of consideration.

Methods for projecting fish and shellfish responses

There are several published methods for incorporating environmental forcing into population dynamics equations (Peterman *et al.*, 2000; Maunder and Watters, 2003; Arregui *et al.*, 2006). Three categories of models hold particular promise for use in projecting climate-change effects on fish and shellfish recruitment. Category 1 models project recruitment (R) by modifying average recruitment ($\bar{R}$) by an environmental variable [I; Equation (1)], where n is the number of variables and their associated constants (a_i). In this case, the environmental variable (s) would be drawn from the projected ensemble from IPCC models output derived using the weighting method described above:

$$R_{y+1} = \left(R_1 \exp\left(\sum_{i=1}^{n} a_i I_{i,y} \right) \exp\left(\varepsilon_y - \sigma_R^2/2\right) \right); \qquad (1)$$
$$\varepsilon_y \sim N(0, \sigma_R^2).$$

The error term ε_y allows the user to project the expected range of variability in recruitment by simulating 50-year recruitment scenarios with random draws from a distribution of expected recruitment. The potential range of process error associated with the selection of climate-change scenarios can be incorporated by

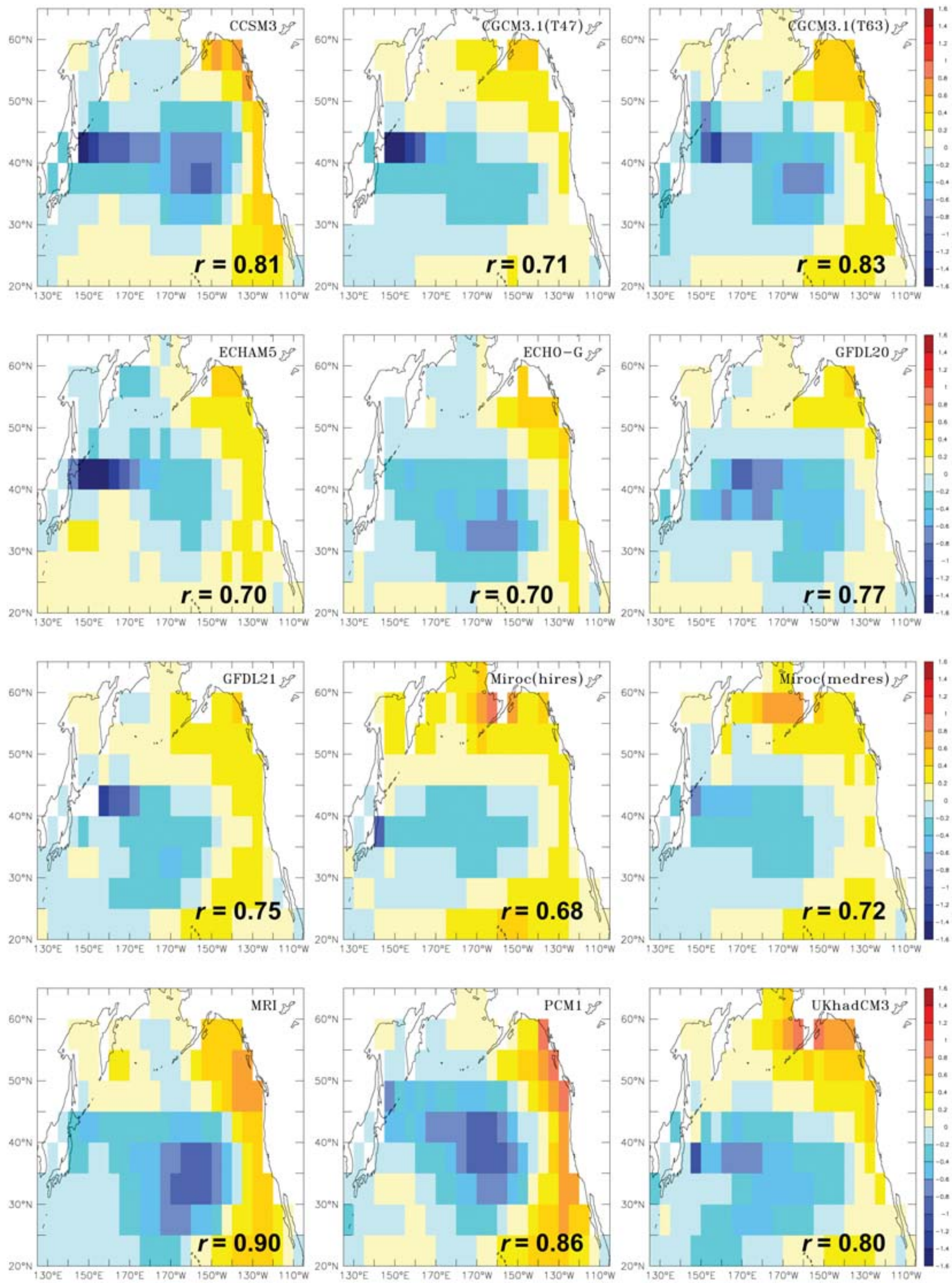

Figure 1. Fit of 12 of 22 IPCC models to the first principal component (Empirical Orthogonal Function; EOF1) of SST in the North Pacific, adapted from Wang *et al.* (in press).

projecting recruitment using different climate-change scenarios and weighting the mean recruitment projections by the weights provided by the retrospective assessment of the performance of the climate models described above. Density-dependent processes are not considered in Category 1 models.

Category 2 models modify the spawner–recruitment relationship with incorporated environmental variables (I) and random variability ε_y (Hilborn and Walters, 1992). For example, a Ricker-type spawner–recruitment model could be constructed as follows:

$$R_t = \left(\alpha * S_t * \mathrm{e}^{-(\beta S + a_1 I_{1,t} + a_2 I_{2,t} + \ldots)}\, \mathrm{e}^{(\varepsilon_y - \sigma_R^2/2)}\right).$$

This approach has been used in several retrospective studies designed to assess the performance of models with and without

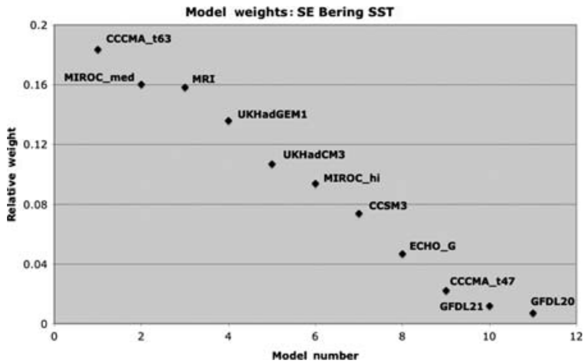

Figure 2. Weights for various models used in forming ensemble mean using a Bayesian model averaging approach. The criteria used for evaluating the models were the accuracy of their hindcasts in terms of reproducing the mean, variance, and trend in the observed SST of the Bering Sea shelf over the last half of the 20th century.

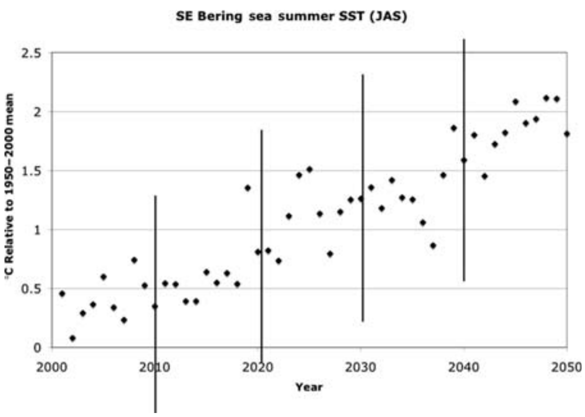

Figure 3. Weighted ensemble mean of IPCC forecasts of SST under A1B emissions scenario. The vertical lines for selected years extend from the mean − 1 s.d. to the mea n + 1 s.d., based on combining the intermodel and intramodel variance in the individual projections.

environmental forcing (Peterman *et al.*, 2000; Wilderbuer *et al.*, 2002). The expected range of variability in recruitment resulting from climate forcing could be simulated by incorporating environmental variables derived from an ensemble of IPCC model outputs derived from the weighting method described above.

Category 3 models utilize spawner–recruitment functions that incorporate processes at multiple life stages. Some species exhibit dynamic and complex processes because of multiple bottlenecks occurring over several life stages (Rothschild, 2000). Phase transitions in the spawner–recruitment relationship may result from time-lags in the recruitment response of predators and prey (Bailey, 2000). Brooks and Powers (2007) proposed a generalized method for modelling the spawner–recruitment relationship when key governing factors are exhibited over several life stages. This modelling approach tracks stage-specific processes and accounts for density-dependent effects on the predation rate. Alternatively, predation effects could be modelled explicitly using a multispecies modelling approach (Jurado-Molina *et al.*, 2005). In Category 3 models, time-series of environmental variables would be derived from ensembles of IPCC model output for different life stages (seasons).

Some ecosystems may exhibit threshold responses (regime shifts) to changing climate conditions (Anderson and Piatt, 1999; Beaugrand *et al.*, 2003; Chavez *et al.*, 2003; Peterson and Schwing, 2003; Scheffer and Carpenter, 2003; Hsieh *et al.*, 2005). Threshold responses (regime shifts) to abrupt shifts in climate may reflect changes in the carrying capacity of the ecosystem. Category 1 models would address shifts in the carrying capacity by partitioning the retrospective time-series into regimes and estimating $\bar{R}$ and σ_R^2 for the different regimes. Shifts in the carrying capacity would be addressed in Category 2 and 3 models by incorporating indicators of prey abundance and habitat volume directly into the spawner–recruitment relationship.

The framework presented here could be modified to assess the implications of climate change on spatial distributions related to range extensions or contractions (Mueter and Litzow, 2008). Shifts in the range or migration patterns of marine fish or shellfish could be incorporated indirectly by including indicators that represent the volume of suitable habitat (Jacobson *et al.*, 2005; Pelletier and Mahévas, 2005; Agostini *et al.*, 2006).

Stock assessment scientists typically project the stock forward to assess the near-term consequences of different harvest strategies (see Punt, 2003; Goodyear, 2004, 2005; Methot, 2005; Schnute *et al.*, 2007, and http://nft.nefsc.noaa.gov/index.html). For Category 2 and 3 models, analysts have the option of estimating parameters for the spawner–recruitment relationship within a stock assessment or outside the stock assessment (Haltuch, 2008; Schirripa *et al.*, 2009). Simulation testing and short-term forecasting is recommended to assess the skill of the model relative to observed responses of fish and shellfish. These tests will provide a measure of the uncertainty associated with the model (Schirripa *et al.*, 2009). Such tests could be incorporated into the periodic stock assessment cycle. Such an approach will allow analysts to adjust the model to incorporate new information.

Management considerations

Projections of the distribution, abundance, and growth of fish and shellfish populations should include scenarios regarding the expected trends in anthropogenic effects (Easterling *et al.*, 2007). Time-trends in the world markets for fish and shellfish are likely to influence the local demand for seafood (Pinnegar *et al.*, 2006). Collaborations with economists and social scientists will be required to develop scenarios for the cost of shipping, food preferences, and new technological innovations for storage and product development. Collaborations with resource managers will be required to develop scenarios for future harvest management practices (A'mar *et al.*, 2009). Scenarios for time-trends in habitat enhancement (e.g. artificial reefs) and stock enhancement (marine ranching) will also be required to forecast the production, distribution, and growth of marine fish and shellfish populations throughout the world adequately.

An application for northern rock sole

Northern rock sole (*Lepidopsetta polyxystra*) is an important flatfish species in the North Pacific Ocean and it has a large biomass in the eastern Bering Sea. The species supports a substantial fishery in the Bering Sea; it is also harvested in the Gulf of Alaska. Temporal trends in northern rock sole production have been found consistent with the hypothesis that decadal scale (or shorter) climate variability influences survival during the early life-history period (Wilderbuer *et al.*, 2002). After spawning in February–March, northern rock sole larvae are subject to

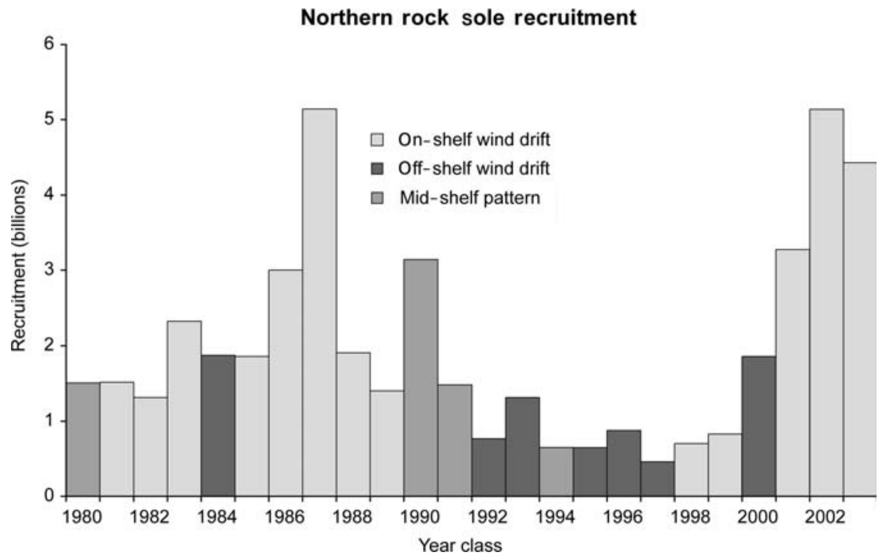

Figure 4. "Observed" recruitment of northern rock sole (estimated from a statistical age-structured model used in the 2007 annual stock assessment). Bar colours reflect classification according to spring climate condition: on-shelf wind drift (lightest shading), off-shelf wind drift (darkest shading), and mid-shelf wind drift (intermediate shading).

advection by wind, currents, and tidal forcing during April–June. Using an ocean surface current model (Ingraham and Miyahara, 1988), Wilderbuer *et al.* (2002) found that wind-driven advection of larvae towards favourable nursery areas in the inner domain coincided with above-average recruitment. The inner domain of the Bering Sea is a productive region because of tidal mixing (Coachman, 1986; McRoy *et al.*, 1986). Ocean forcing resulting from on-shelf (easterly) winds during the 1980s, and again in 2001–2003, coincided with periods of above-average recruitment, whereas off-shelf (westerly) or mid-shelf (northerly) winds during the 1990s corresponded to periods of poor or average recruitment (Figure 4). This suggests that patterns of future recruitment for northern rock sole would depend on wind patterns that are influenced by future climate conditions. Therefore, to predict future recruitment for northern rock sole, it is also necessary to predict future climate conditions.

Following the framework for projecting environmental variables outlined above, spring wind, and the associated advection on the Bering Sea shelf, was estimated from a weighted ensemble of IPCC model output. Again, the various IPCC models used were rated based on how well their hindcasts for the latter half of the 20th century matched observations. The two specific criteria for this rating were the IPCC model's ability to reproduce the overall mean April–June winds on the southeast Bering Sea shelf, and the interannual variance in the seasonal mean winds. In general, the models were able to hindcast the winds more accurately than the SST. The normalized errors in the modelled mean and variance in the winds ranged from ~0.1 to 2. In addition, a different ranking emerged for the climate models for the cross-shelf wind index (Figure 5) than for the late summer SST example presented earlier (Figure 2). Although the MIROC-med and MRI models ranked high for both parameters, the ECHO-G ranked low for both. Other models, such as the CCCMA_t63 and GFDL2.1, were decidedly better for one parameter than for the other. The weights for each model with respect to the cross-shelf winds were then used to form a projection of the winds

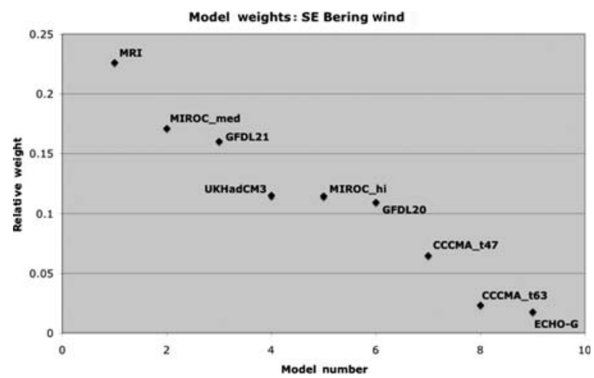

Figure 5. Weights for various models used in forming ensemble mean using a Bayesian model averaging approach. The criteria used for evaluating the models were the accuracy of their hindcasts in terms of reproducing the mean, variance, and trend in the observed wind of the Bering Sea shelf over the last half of the 20th century.

out to 2050 and converted to ending longitude of surface-drifting larvae. These projections, with the attendant year-to-year variability provided by the Bayesian scheme, indicated a slight tendency towards increased shoreward transports, with substantial variability on top of this weak trend (Figure 6).

Based on these results from the IPCC climate models, the future production of northern rock sole was projected for the period 2001–2050 using a method similar to the Category 1 recruitment function. A hierarchical bootstrap algorithm was applied to estimate annual variability in future spring climate (i.e. wind direction and subsequent larval drift), as well as variability in recruitment under a given climate condition. First, three climate conditions (corresponding to the three production regimes identified by Wilderbuer *et al.*, 2002) were characterized according to the range of the ending longitude (L) expected for larval drift under each condition: (i) on-shelf drift ($L < 165°$W),

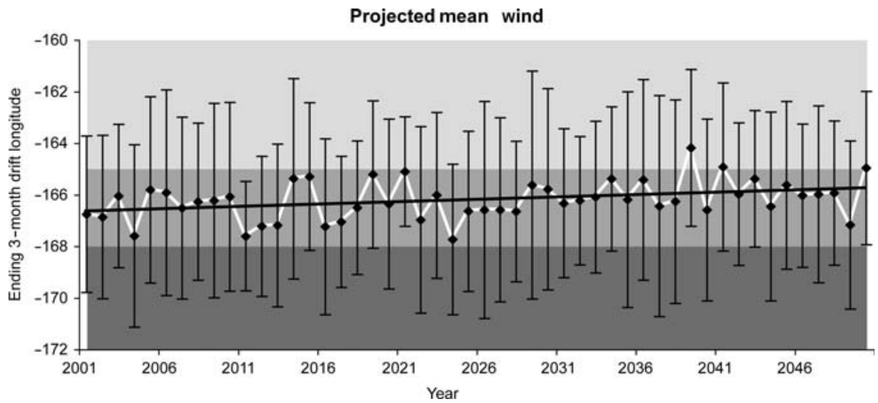

Figure 6. Predicted mean and standard deviation of the longitudinal endpoint of projected larval drift from spring winds for 2001–2050. Background plot shading reflects classification of projected endpoints according to spring climate condition: on-shelf wind drift (lightest shading), off-shelf wind drift (darkest shading), and mid-shelf wind drift (intermediate shading).

(ii) mid-shelf drift (165°W < $L \leq$ 168°W), and (iii) off-shelf drift (168°W $\leq L$). Then, for each projected year, the corresponding predicted mean drift-ending longitude and variance from the IPCC model results were used (Figure 6) to draw a sample ending drift longitude from a normally distributed population. Next, the climate condition corresponding to the sample longitude was identified, based on the limits presented in Figure 6. Finally, a value for recruitment was randomly selected (with replacement) from the set of "observed" recruitments (Figure 4) corresponding to the given climate condition. This was repeated 20 000 times to generate bootstrap realizations for each projected year. For each year, the probability of occurrence for each climate condition was computed (Figure 7), as well as the mean and distribution of recruitment (Figure 8).

Not surprisingly, the temporal trend in probability of occurrence of each climate scenario followed a pattern similar to that of the mean ending longitude of larval drift. These results suggest a moderate increase in expected recruitment over time, because the trend indicated more frequent occurrence of the on-shelf climate condition (A in Figure 7) over time, which corresponds to the highest expected mean recruitment. However, Figure 7 does not incorporate the variation in recruitment, which is displayed in Figure 8.

Once the variation of recruitment within a climate condition was incorporated, any trend towards larger recruitments over time was much reduced (Figure 8). The mean of expected recruitment displayed a comparatively smaller trend towards larger values over time, whereas the median displayed no trend whatsoever. The reduction in trend from mean to median happened because of the asymmetrical nature of the distribution of recruitment under each of the three climate conditions. As such, the model suggests that, to the best of our current knowledge, rock sole production will not be substantially affected by future climate change—at least concerning the effects of that change on patterns of spring larval advection.

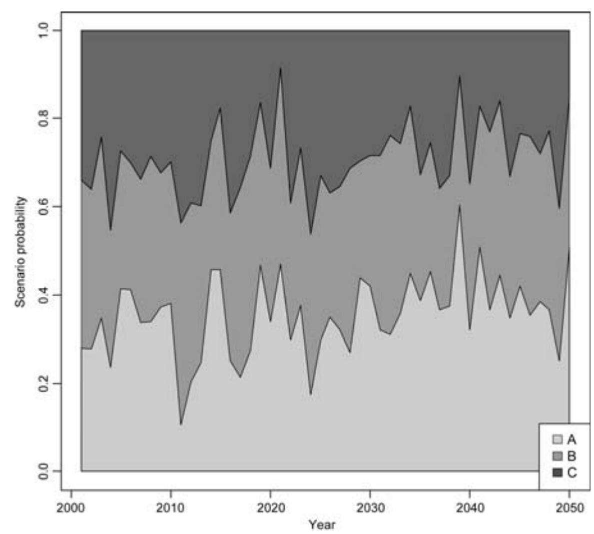

Figure 7. Cumulative probability of future spring climate conditions (A, B, and C) based on 20 000 bootstrapped samples year^{-1} (A, onshore winds; B, mid-shelf winds; C, offshore winds).

Discussion

A framework for forecasting the implications of climate change on production of marine fish that incorporates estimates of key environmental variables derived from IPCC GCM outputs in stock projection models is presented. The wide range of possible outcomes from the AR4 models presents a challenge. To deal with possible systematic errors in these models and the uncertainty in their simulations in general, a method was developed for weighting individual model forecasts. This method yields estimates of means and variances in environmental variables projected into the future on the time- and space-scales relevant to fish and shellfish populations. The framework also utilizes known linkages between environmental variability and fish and shellfish production. Statistical-projection methods allow scientists to simulate the likely effects of climate change on fish and shellfish, incorporating the uncertainty associated with climate projections and process error in the projection model. Stock projection models are utilized to project the expected value and its associated uncertainty.

There is considerable debate about the best practices for downscaling IPCC model output for use in projecting the effects of climate change on marine ecosystems (ICES, 2008). Comparison of the model weights for summer SST and spring winds illustrates that IPCC GCMs have different strengths and weaknesses for

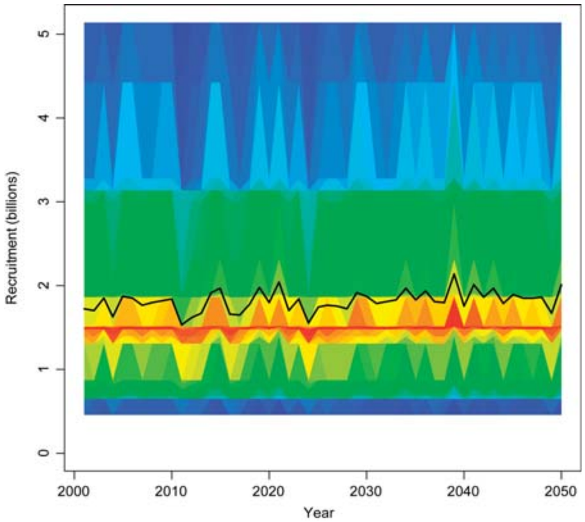

Figure 8. Projected mean (black line) and quantiles (coloured shading) for northern rock sole productivity (recruitment) by year. Quantiles are colour-coded symmetrically from the median (bright red) to 0 or 100% (dark blue).

projections for the Bering Sea. The Bayesian weighting technique suggested herein is designed to limit the use of unrealistic and improbable climate trajectories. The use of a pre-simulation skill assessment should also reduce uncertainty that arises from structural incompleteness in the models (ICES, 2008). Importantly, it allows for the estimation of error bounds and for quantifying levels of confidence.

Future work could evaluate results using alternative selection processes and weighting schemes. For example, Tebaldi and Bruno (2009) present an alternative Bayesian-modelling approach to estimate uncertainty in ensembles of climate models. In some cases, the environmental variable needed for projection may not be readily available from IPCC model output. When this occurs, analysts will have to determine the empirical relationships linking climate forcing to regional biologically relevant variables, as well as the associated uncertainty. These relationships could be used to improve the estimates of time-series of environmental variables derived from ensembles of IPCC climate-model output and will provide a measure of the associated uncertainty in the projections resulting from downscaling.

We acknowledge that some doubts remain about the credibility of the GCMs being used for climate projections. For example, Koutsoyiannis *et al.* (2008) compared the 20th century hindcasts from a variety of models with observations and found a mismatch on decadal time-scales. We contend that this was not a valid test of the models, because of the chaotic nature of the climate system. The lack of predictability for specific events (e.g. relatively warm or cool conditions for a particular region and time interval) does not imply that the models cannot be used to anticipate overall changes in the properties of the climate from a stochastic perspective.

As for stock assessment models, the approach described here is a simplification of the complex processes controlling population responses to climate drivers. The predictive skill of climate models is uncertain and this uncertainty is likely to grow over time, making simulations at the end of the time-series less reliable (Smith *et al.*, 2007). When coupled with the possibility of behavioural, genetic, or other forms of adaptation, uncertainty is further increased. However, Levin *et al.* (1997) recommended that mechanistic models should be developed that begin with what is understood (or hypothesized) about the interactions of individual units, with a goal to identify emergent behaviour that can be expressed as statistical ensembles. The framework presented in this paper encourages scientists to build on the long history of fisheries oceanographic research available in many of the world's large marine ecosystems to formulate scenarios for potential effects of climate change on marine fish and their fisheries.

The framework relies on existing knowledge of linkages between environmental forcing and fish production, and these linkages may be unreliable. The effects of short-, medium-, and long-term environmental influences on fish stocks are complex and uncertain for most species, and predictions of stock status are dependent upon accurate forecasts of the appropriate environmental indices and the stability of the relationships between climate and the stock (Fréon *et al.*, 2005). There are many examples where proposed relationships between fish or shellfish recruitment and climate have not held up over time (Myers, 1998; Bull and Livingston, 2001; De Oliveira and Butterworth. 2005; Francis *et al.*, 2006). The imprecision inherent in the projections of climate–recruitment relationships can be attributed to: (i) misspecification of or changes over time in the links between climate and recruitment; (ii) error and uncertainty in estimating the characteristics of the links based on historical data; and (iii) error and uncertainty in the forecasts of the climate indices. Francis (2006) suggests that cross-validating the environmental variables included as influences on stock dynamics may assist in determining more reliable relationships between recruitment and climate. Relationships may also fail when ecosystem linkages have non-linear underpinnings (Scheffer and Carpenter, 2003). To address this issue, time-series could be analysed to assess the dimensionality of the system at different time-scales (Sugihara and May, 1990; Sugihara, 1994; Hsieh *et al.*, 2005).

The framework for projecting climate-change effects on fish and shellfish presented here was intentionally designed to parallel the modelling approach used for stock assessment. The expectation is that the parameters and functional forms assumed for stock assessment will be regularly evaluated as part of the public review of stock assessments and the active peer review of fisheries oceanographic research. As understanding of the functional relationships between environment and fish production evolves, this information can be rapidly updated in the climate-change projections. As part of the periodic reviews, skill assessments could become an integral aspect of the proposed framework to update models continually as new information is acquired (Stow *et al.*, 2009).

There are alternative modelling approaches that could be considered for forecasting climate-change effects on commercial species. As mentioned in the Introduction, it is also possible to conduct experiments involving integrated dynamical models. For example, Rose *et al.* (2006) coupled a regional ocean circulation model with a nutrient–phytoplankton–zooplankton component to an individual-based model with bioenergetic models to explore the implication of changes in ocean forcing on fish growth. This type of model could be modified to investigate the effects of climate change by treating the IPCC model output as boundary and initial conditions for a regional ocean model. Numerical "experiments" could be performed with the biophysical model under different climate scenarios to develop the environmental variables for use in stock projection models (e.g. Category 2 model) or outputs could be drawn from trophically linked spatial models. Levin *et al*. (1997) suggested that this class of model system should be used when the added amount of detail can be supported by observations that can be measured. The detailed information needed for validation and parameterization of dynamic models is difficult and expensive to collect, as illustrated by the ambitious effort underway in the Bering Sea under the auspices of the Bering Sea Integrated Research Program (BSIERP)-Bering Sea Ecosystem Study (BEST) programme (http://bsierp.nprb.org).

The forecasting framework was applied for the Bering Sea region to demonstrate the method for selecting IPCC model output and developing a weighted ensemble for an environmental variable of interest (July–September SST). This method revealed that the CCCMAT-63 and the MIROC-M models produced the most accurate estimates of mean, variance, and trends in Bering Sea SST for the last half of the 20th century. The weighted ensemble demonstrated that mean SSTs are expected to increase by 2°C by 2050. This implies that a typical summer in 2050 will be as warm as the warmest summers of the present day (Overland and Stabeno, 2004). These changes are likely to affect the spatial distribution of many fish and shellfish populations in the region (Mueter and Litzow, 2008) and could affect the seasonal production cycle (Hunt *et al*., 2002).

The effect of climate change on Bering Sea northern rock sole production provides an example of the Category 1 forecast. Specifically, the model incorporated uncertainty at the level of both future climate change and the biological response to that climate. The results suggested that qualitative forecasts of the effect of climate on fish and shellfish based singly on IPCC model scenarios (Figure 7) could overestimate the biological response (Figure 8). Incorporating the distribution of recruitments under different climate regimes into the forecast contributed to the perception of the climate effect.

Several assumptions were necessary to complete the example forecast. For simplicity, recruitment was assumed independent of stock size. This allowed bootstrapping over recruitments within a climate scenario, rather than using deviations from a climate-specific stock–recruitment relationship. As such, projections of future stock size were not needed. A more sophisticated model, which incorporates climate-mediated changes in density-dependence, would be an example of a Category 2 model. Such a model might incorporate additional realism by including serial autocorrelation in recruitment through its dependence on stock size, but at the expense of added complexity associated with projecting stock size from one year to the next.

The example model incorporated only the effect of projected changes in cross-shelf transport on recruitment of northern rock sole. Changes in SST are not expected to change the tidal mixing that occurs in the inner domain, which creates a nutrient-rich nursery area for northern rock sole. Furthermore, retrospective studies established that SST was not significantly related to recruitment (Wilderbuer *et al*., 2002). We therefore expect that changes in SST will not have a strong effect on recruitment of northern rock sole and that cross-shelf transport will continue to be the most influential environmental variable influencing it.

The northern rock sole example forecast recruitment based on our current understanding of the linkages between climate and recruitment. Other processes (e.g. prey availability, growth, and predation rates) could be influenced by increases in SST. For northern rock sole, retrospective studies did not provide evidence that recruitment was significantly influenced by warm surface temperature. If evidence becomes available, these temperature effects on processes could be addressed using a Category 2 or 3 model that tracks, for example, the effect of temperature on the dynamics of growth through the population. However, because the functional form and parameter values for this temperature dependence are unknown for northern rock sole, developing a model that incorporates SST would be purely hypothetical. Until the requisite field and laboratory experiments necessary to elucidate linkages are undertaken, incorporating temperature effects would remain an academic endeavour. Expanded field and laboratory studies are needed to evaluate the potential response of fish to projected environmental conditions.

Stochastic simulations allow for a comparison of the mean and median estimates of recruitment over time. In the next 10–20 years, interannual and decadal scale variability is likely to dominate trends in cross-shelf transport of northern rock sole larvae. Recruitment of this species is likely to continue to vary. After 2025, mean recruitment is expected to trend upwards at a modest rate, whereas the median recruitment is expected to remain stable. The reduction in trend from mean to median stems from the asymmetrical nature of the distribution of recruitment under each of the three climate conditions.

The examples presented here address the uncertainty resulting from model selection, environmental process error, measurement error in the assessment, and process error in the spawner–recruitment relationship. In our analysis, process error in the spawner–recruitment relationship was incorporated using a bootstrap method. An alternative approach would be to estimate the probability distributions for parameters used in the relationship between the environment and recruitment, to provide an estimate of the parameter uncertainty as an addition to the process and observation error already inherent within the framework.

If interdisciplinary research teams around the world use this or a similar framework to assess climate-change effects on marine fish and shellfish, comparative studies can be used to evaluate hypothesized relationships. Myers (1998) advocated this approach, suggesting that hypothesized relationships could be verified and validated with separate tests and analyses, using meta-analyses across ecosystems, geographical areas, and/or species to explore other links between climate and recruitment. If regional modelling teams apply the framework and meet to compare results, we anticipate that a more comprehensive assessment of climate-change effects on the availability of fish and shellfish resources throughout the world will be available for consideration by future IPCC review panels.

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