ARTICLE

Decadal changes in the productivity of New England fish populations

Adrien Tableau, Jeremy S. Collie, Richard J. Bell, and Cóilín Minto

Abstract: The Northwest Atlantic continental shelf is a large ecosystem undergoing rapid environmental changes, which are expected to modify the productivity of natural marine resources. Current management of most fished species assumes stationary production relationships or time-invariant recruitment rates. With linear state-space models, we examined the evidence of dynamic productivity for 25 stocks of the Northeast US shelf. We expanded the suite of options available within the state-space approach to produce robust estimates. Fifteen of the stocks exhibited time-varying productivity or changes in their maximum reproductive rate. Few productivity time series are related across the whole region, though adjacent stocks of the same species exhibited similar trends. Some links to region-wide environmental variables were observed. We demonstrate that fish recruitment can often be better predicted over a short-term horizon by accounting for dynamic productivity, which could be valuable for fisheries management. Improving predictions by incorporating environmental covariates or covariance among the stocks must be considered case by case and with caution, as their relationships may change over time.

Résumé: Le plateau continental de l'Atlantique Nord-Ouest est un vaste écosystème subissant des changements environnementaux rapides. Ces derniers sont suspectés de modifier la productivité des ressources marines naturelles. Cependant, la gestion actuelle des espèces de poissons est basée sur des relations de productivité constantes ou des taux de recrutement constants. A l'aide de modèles linéaires à espace d'état, la pertinence d'une productivité dynamique est étudiée pour 25 stocks de poissons du plateau Nord-Est des USA. Des estimations robustes ont été produites en développant l'approche espace-état. Quinze des stocks étudiés présentent une productivité, ou taux maximum de reproduction, variant dans le temps. Au sein de cet écosystème, la productivité des stocks varie rarement de façon semblable. Seuls les stocks d'une même espèce localisés dans des zones adjacentes présentent des tendances similaires. Les variables environnementales régionales expliquent très peu la variabilité temporelle. Nous démontrons que le recrutement est souvent mieux prédit à court terme avec une productivité dynamique, ce qui peut être valorisable pour la gestion des pêches. Pour améliorer la prédiction, l'utilisation de covariables environnementales ou de la covariance entre les stocks doit se faire au cas par cas. Comme ces relations ne persistent pas toujours dans le temps, leur utilisation doit faire l'objet de précautions préalables.

Introduction

Productivity — the capacity of a fish population to increase in numbers and mass — is affected by variations in the recruitment rate, body growth, and survival success (Shelton et al. 2006). The realized production also depends on population density, age structure, and ambient environmental conditions. We focus here on that part of the productivity depending on the reproduction rate because recruitment variability is the largest source of variation in marine fish populations (Sissenwine 1984). For brevity, we use the term productivity to represent the maximum reproductive rate. The productivity of many marine fish species, including Pacific salmon (Peterman et al. 2003) and Atlantic cod (Gadus morhua) (Minto et al. 2014), among others, has been shown to vary markedly on decadal time scales. Recent trends in productivity have been attributed to the combined effects of environmental change and overfishing (Britten et al. 2016).

The latent productivity is generally measured by the maximum reproductive rate in a surplus-production or stock-recruitment model (Quinn and Deriso 1999). In age-structured populations, productivity can be measured as the ratio of recruits (R) per spawner (S) or its logarithm. Changes in productivity can be reflected directly by R/S but also depend on stock density (S). Inter-

annual changes in productivity may be reflected in the residuals between observed log(R/S) and the model estimates from a stock-recruitment relationship. Persistent changes in productivity are indicated by strings of positive and negative residuals. These persistent changes can be captured with a dynamic version of the Ricker model, which allows the parameters to vary over time and to be estimated with a Kalman filter (Peterman et al. 2003). The linearized form of the Ricker model permits the use of the Kalman filter, which is a special case of state-space models. This approach is fundamentally different than assuming autocorrelated errors in the stock–recruitment function, as it captures the recursive change of the recruitment instead of representing the short-term memory in the error process (Minto et al. 2014).

What are the most likely causes of fluctuations in productivity? Having accounted for harvesting and population density, environmental variability, including climate change, becomes the most likely driver (Shelton et al. 2006; Richardson et al. 2014). Numerous fish stocks in the Northeast US continental shelf ecosystem have been identified as vulnerable to climate change (Hare et al. 2016). The cold Labrador Current from the north and the warm Gulf Stream from the south meet in this region and influence its physical dynamics (Greene et al. 2013). This highly productive

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ecosystem exhibits strong seasonal dynamics (Sherman et al. 1996). The exploited fish are largely demersal species characterized by a range of lifespans (9 to 50 years) (Froese and Pauly 2000). Many exhibit seasonal migrations between coastal and deeper waters, and while a number spawn in the spring, there is a wide diversity of spawning seasons across the Northeast US shelf taxa (Fahay and Able 1989). The region has been heavily exploited in the past and is experiencing rapid climatological changes (Fogarty and Murawski 1998; Ecosystem Assessment Program 2012). Relationships between productivity and climate variables have been identified for some stocks, including cod (Fogarty et al. 2008), winter flounder (Pseudopleuronectes americanus) (Bell et al. 2014) and yellowtail flounder (Limanda ferruginea) (Sissenwine 1974). For a subset of these stocks, a mechanism relating temperature to survival has been identified (Hare et al. 2010; Bell et al. 2018). As temperature is a major determinant of energy allocation, given its impact on metabolism (Manderson 2016), temperature increases may therefore be expected to result in changing fish productivity (Bell et al. 2014).

Multiple stocks of the same species (Peterman et al. 2003; Manderson 2008; Minto et al. 2014) or different species in the same ecosystem may have patterns in productivity that covary in time. In these cases, multistock models can be useful to estimate the shared productivity pattern and to inform the productivity estimates for stocks lacking recent assessments. Further, the multistock approach can provide an understanding of the scale and similarity–dissimilarity of productivity response of similar species across regions and different species within a region, thus providing insights into the scale of plausible hypotheses to explain given changes (Minto et al. 2014).

Biological reference points that are used to assess stock status are calculated from contemporary life-history parameters, which are periodically updated in benchmark assessments. Recruitment is generally assumed to follow a time-invariant distribution based on the entire time series within a single assessment model. As long as changes in productivity are high-frequency and uncorrelated (e.g., residuals of a stock-recruitment model), time-invariant reference points average out the environmental variability (Peterman et al. 2000). But when persistent deviations are observed over several years, reference points may need to be adjusted to account for changing productivity. Time-varying harvest policies that respond to changing productivity can, in some cases, outperform corresponding time-invariant policies (Collie et al. 2012). Dynamic harvest policies are based on productivity forecasts. Model selection criteria, which are based on goodness of fit, do not always select the model providing the best forecasts (Chatfield 1996). It is thus necessary to also estimate the forecast accuracy of models to judge their utility.

The main objective of this study is to derive robust estimates of productivity for a suite of fish stocks in the Northeast US continental shelf ecosystem. We test whether the productivity patterns can be described by linear trends or explained with hypothesized climate drivers. Finally, we apply a multistock approach to test for covariation in productivity patterns. We extend current methods that simply investigate whether productivity has changed to questions of how has productivity changed within and across areas and species; are there potential drivers of observed change; and what is our ability to forecast such changes over different time horizons?

Materials and methods

To understand if stock productivity changed over time, we fit a time-varying Ricker stock—recruitment model within a state-space framework (Peterman et al. 2003). In the baseline case, the statespace model enabled the fitting of a dynamic productivity term that was compared with a standard, time-invariant Ricker model. The baseline, time-varying model was then extended in an attempt to understand how dynamic productivity evolves in time and how well we can predict future changes. We incorporated a linear drift term as well as environmental covariates to determine if they improved the predictive ability (environment-driven models). Additionally, we examined the covariance structure among the productivity of species on the Northeast US shelf to determine whether there were broad patterns across the stocks and whether information from other fish stocks could be used to improve the forecast of productivity for a given stock.

Recruitment and spawning stock biomass (SSB) estimates

SSB and recruitment time series come from stock assessment outputs issued by the Northeast Fisheries Science Center (NEFSC-NOAA) (refer to online Supplementary material, Table S11). Information was available for 25 fish stocks on the Northeast US continental shelf (Table 1 and Fig. 1). Recruitment time series were lagged by the age-at-recruitment to match recruits with their spawners (e.g., if R is the recruitment estimate in year 2000, and age-at-recruitment is 3 years, R is associated with the spawning stock in 1997). Stocks were divided into three general groups based on their life history and taxonomy, with the expectation that species with similar life history or taxonomy may exhibit similar productivity patterns over time. Species were thus divided into a pelagic group, which corresponds to fish living exclusively in the water column, a flatfish group, which is benthic (Moyle and Cech 2004), and a roundfish demersal group, defined here by all the other species living on or near the bottom.

Climate data

Changes in the environment can drive variations in productivity (Klein et al. 2017; Perretti et al. 2017). Four climate variables were selected because previous studies have suggested they may be related to the productivity of fish stocks from the Northeast US continental shelf and because they are available within the same time frame as the fish data time series (Table 2 and Fig. 2). We tested sea surface temperature, the North Atlantic Oscillation (NAO), the mid-Atlantic cold pool, and the Gulf Stream North Wall index. The sea surface temperature time series is defined by averaging the temperature data over the area of the Northeast US continental shelf. For each species, we tested a specific hypothesis based on previous studies regarding the impact of temperature on recruitment. If previous studies did not exist, we examined the mean seasonal temperature for the season when larvae were present on the Northeast shelf (Table 1). Environmental drivers were reviewed in Hare et al. (2016) and references within. The winter NAO is the dominant atmospheric process having a lagged effect on water temperature and wind on the Northeast US shelf. The mid-Atlantic cold pool is a residual area of colder winter water that remains in the mid-Atlantic - southern New England area into the summer due to stratification. The size and longevity of the cold pool have been linked with recruitment of stocks on the Northeast US shelf (Miller et al. 2016). The latitudinal position of the Gulf Stream North Wall indicates the relative strength of the two currents meeting in the Northeast US shelf. See Xu et al. (2018) for more details on these climate variables and their potential influence.

State-space model

Baseline models

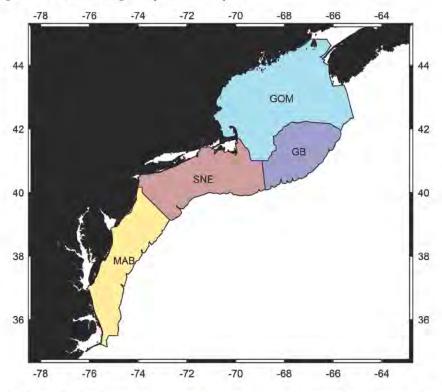
The method to compute time-varying productivity was developed by Peterman et al. (2003) and extended by Minto et al. (2014), who developed a multistock method. The recruits-to-spawners

Table 1. Metadata on the fish stocks of the Northeast US continental shelf.

Common name	Scientific name	Stock area	ID	Age at recruitment	Time span	SST season
Acadian redfish	Sebastes fasciatus	Northeast US shelf	ACA.RED.F_UNIT	1	1960-2014	Summer
American plaice	Hippoglossoides platessoides	Gulf of Maine - Georges Bank	AME.PLA_GB-GM	1	1980-2015	Winter
Atlantic herring	Clupea harengus	Northeast US shelf	ATL.HER_UNIT	1	1965-2014	Summer
Atlantic wolffish	Anarhichas lupus	Northeast US shelf	ATL.WOL_UNIT	1	1968-2014	Winter
Bluefish	Pomatomus saltatrix	Northeast US shelf	BLU.F_UNIT	0	1985-2014	Summer
Butterfish	Peprilus triacanthus	Northeast US shelf	BUT.F_UNIT	0	1989-2012	Summer
Cod	Gadus morhua	Georges Bank	COD_GB	1	1978-2014	Summer
Cod	Gadus morhua	Gulf of Maine	COD_GM	1	1982-2014	Summer
Haddock	Melanogrammus aeglefinus	Georges Bank	HAD_GB	1	1962-2015	Summer
Haddock	Melanogrammus aeglefinus	Gulf of Maine	HAD_GM	1	1977-2014	Summer
Monkfish	Lophius americanus	Gulf of Maine	MON.F_N	1	1980-2011	Summer
Monkfish	Lophius americanus	Georges Bank – southern New England – mid-Atlantic	MON.F_S	1	1980-2011	Summer
Pollock	Pollachius virens	Northeast US shelf	POL_UNIT	1	1970-2014	Winter
Scup	Stenotomus chrysops	Northeast US shelf	SCU_UNIT	0	1984-2014	Summer
Silver hake	Merluccius bilinearis	Northeast US shelf	SIL,HAK_UNIT	1	1973-2009	Summer
Striped bass	Morone saxatilis	Northeast US shelf	STR.BAS_UNIT	1	1982-2012	Winter
Summer flounder	Paralichthys dentatus	Northeast US shelf	SUM.FLO_UNIT	0	1982-2012	Winter
Tilefish	Lopholatilus chamaeleonticeps	Northeast US shelf	TIL.F_UNIT	1	1971-2012	Summer
White hake	Urophycis tenuis	Northeast US shelf	WHI.HAK_UNIT	1	1963-2014	Summer
Winter flounder	Pseudopleuronectes americanus	Georges Bank	WIN.FLO_GB	1	1982-2015	Winter
Winter flounder	Pseudopleuronectes americanus	Southern New England - mid-Atlantic	WIN.FLO_SNE-MA	1	1981-2014	Winter
Witch flounder	Glyptocephalus cynoglossus	Northeast US shelf	WIT.FLO_UNIT	3	1982-2015	Winter
Yellowtail flounder	Limanda ferruginea	Georges Bank	YT.FLO_GB	1	1973-2014	Winter
Yellowtail flounder	Limanda ferruginea	Gulf of Maine - Cape Cod	YT.FLO_GM-CC	1	1985-2015	Winter
Yellowtail flounder	Limanda ferruginea	Southern New England - mid-Atlantic	YT.FLO_SNE-MA	1	1973-2014	Winter

Note: SST season indicates which seasonal sea surface temperature index was tested in the environment-dependent models.

Fig. 1. Sector areas of the Northeast US continental shelf: GOM, Gulf of Maine; GB, Georges Bank; SNE, southern New England; MAB, mid-Atlantic Bight. Coordinates are in degrees of latitude and longitude. [Colour online]



ratio can be described by the Ricker model (Ricker 1954) (see eq. 1). The Beverton–Holt model is sometimes used in assessments (NEFSC 2015; Miller et al. 2016), but the linearization differs from the Ricker model and requires gamma-distributed errors (Minto et al. 2014). The Ricker model depends on two parameters: a maximum-productivity coefficient and a density-dependent coef-

ficient. The general idea in this study is to apply a Kalman filter to the Ricker model to define the variations of the maximum-productivity parameter (hereinafter called productivity). The Kalman filter is an optimal filter for linear, Gaussian models.

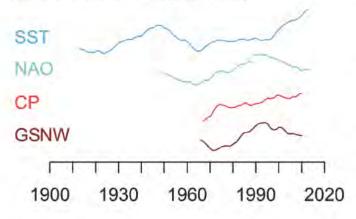
A preliminary step consists of linearizing the Ricker function:

Table 2. Metadata of climates covariates.

Climate covariate	ID	Time span	Period considered	Time lag	Source
Extended reconstructed sea surface temperature	SST	1854-2017	Summer-winter	0 year	Huang et al. 2014
North Atlantic Oscillation index	NAO	1948-2017	Winter	1 year	Barnston and Livezey 1987
Cold pool index	CP	1968-2013	Yearly	0 year	Miller et al. 2016
Gulf Stream North Wall index	GSNW	1966-2010	Yearly	0 year	Taylor 2011

Note: Time lag is relative to year of recruit birth: a 0-year lag for the temperature means that we focus on the temperature of the first summer of the young-of-the-year fish.

Fig. 2. Smoothed and scaled time series of climate variables: SST, sea surface temperature; NAO, North Atlantic Oscillation; CP, cold pool; GSNW, Gulf Stream North Wall (see text for variable descriptions). Smoothing is done with the standard process of the Kalman filter (Petris et al. 2009). [Colour online.]



(1)
$$R_{i,t} = S_{i,t}e^{a_{i,t}}e^{b_{i}S_{i,t}+v_{i,t}} \rightarrow \ln(R_{i,t}/S_{i,t}) = a_{i,t} + b_{i}S_{i,t} + v_{i,t}$$

where $R_{i,t}$ is the recruitment lagged by the age-at-recruitment to the fish stock, $S_{i,t}$ is the spSSB, $a_{i,t}$ is the productivity, b_i is the density-dependent mortality, which is assumed to be time-invariant, and $v_{i,t}$ is observation error. The subscript $i=1,\ldots,I$ indexes the stocks, and t is time in years. $\ln(R_{i,t}|S_{i,t})$ is then simplified as $y_{i,t}$.

It can often be difficult to separately estimate process and observation error variances from a single time series of observations. To address this difficulty and to improve the robustness of the state-space approach for short time series, we extended the original technique (Peterman et al. 2000; Dorner et al. 2008; Collie et al. 2012) by estimating parameters for all the stocks on the Northeast US together with a single signal-to-noise ratio (ratio of process-error variance to observation-error variance). For a single stock *i* among the *I* stocks, the model is defined with diffuse priors on the states (see section on Model initialization below) and two model equations: the observation model (eq. 2), and the process model (eq. 3), which is a simple random walk, as used in previous studies.

(2)
$$y_{i,t} = a_{i,t} + b_i \cdot S_{i,t} + v_{i,t}$$
 with $v_{i,t} \sim N(0, \sigma_{v_i}^2)$

(3)
$$a_{i,t} = a_{i,t-1} + w_{i,t}$$
 with $w_{i,t} \sim N(0, \sigma_{w_i}^2)$

A matrix form is used to describe the multistock model:

(4)
$$Y_t = F_t X_t + v_t$$
 with $v_t \sim N(0, V)$

(5)
$$X_t = G_t X_{t-1} + w_t$$
 with $w_t \sim N(0, W)$

where $Y_t = (y_{1_t}, y_{2_t}, ..., y_{I_t})'$ is the observed state of $\ln(R_{i,t}/S_{i,t})$ for each species, and $X_t = (a_{1,t}, a_{2,t}, ..., a_{I,t}, b_1, b_2, ..., b_l)'$, with a being the

time-varying productivity term for each species and b being the density-dependent parameter, implemented here as time-invariant. Matrix \mathbf{F}_t defines the Ricker function. It is two diagonal matrices of dimensions $I \times I$ side by side; the dimensions of \mathbf{F}_t are $I \times 2I$. The values of the first diagonal are 1; the second diagonal values are the SSB: $S_{1,t}, S_{2,t}, \dots S_{I,t}$. Matrix \mathbf{G}_t describes the link between two successive states; it is an identity matrix with dimensions $2I \times 2I$. The total variance in Y_t is partitioned into three sources: density dependence $(S_{i,t})$, estimation error (v_t) , and process error (w_t) . The error vectors follow the multivariate normal distributions defined by the covariance matrices \mathbf{V} and \mathbf{W} of dimension $I \times I$ and $2I \times 2I$, respectively. Matrix \mathbf{W} describes the intensity of the process evolution (variance parameters) and the relationship between the processes (covariance parameters). \mathbf{W} is defined as $\mathbf{W} = \begin{bmatrix} \mathbf{W}_a & \mathbf{0}_{ab} \\ \mathbf{0}_{ba} & \mathbf{0}_b \end{bmatrix}$ with each submatrix, \mathbf{W}_a , $\mathbf{0}_{ba}$, $\mathbf{0}_{ab}$, and $\mathbf{0}_b$, having dimensions $I \times I$.

Two models are tested:

 The simplest model defines a time-invariant productivity; it is the equivalent of a simple invariant Ricker model (called invariant model):

$$\mathbf{W}_a = \mathrm{diag}(0,0,...,0)$$
 and $\mathbf{V} = \mathrm{diag}(\sigma^2_{v_1},...,\sigma^2_{v_l})$

2. A model with a time-varying productivity (called varying model):

$$\mathbf{W}_{a} = \operatorname{diag}(\sigma_{w_{1}}^{2}, \sigma_{w_{2}}^{2}, ..., \sigma_{w_{l}}^{2})$$

For the time-varying productivity model, likelihood maximization supplies estimated standard deviations for both observation and process errors. For each stock, the likelihood is very flat around its maximum (see Fig. S11). This suggests that disentangling observation error from process error is not robust given the limited length of the data time series, and thus their estimates could be widely influenced by the starting values (Petris et al. 2009). To achieve robust estimates, we assumed a common signalto-noise ratio among fish stocks (i.e., the ratio of the standard deviations of process and observation errors; snr). By assuming a common signal-to-noise ratio among the stocks and estimating it within the model, we reduced the number of estimated parameters from 2I to I + 1 parameters (I process error variances and one snr) and consequently increased the robustness of the output. This assumption enabled consistent parameter estimates within reasonable confidence intervals for all stocks (see Fig. S11). Matrix V is then defined as

$$V = diag(W_a)/snr^2$$

Model initialization

Models are also defined by the initialization of the states. For each stock i, this step requires priors for $a_{i,0}$ and b_i . For the prior means, we fit the simple linear model (a_i' and b_i' are constant parameters):

$$y_{it} = a'_i + b'_i \cdot S_{it}$$

The estimate of b_i' is used for the mean of the b_i priors. As the productivity is time-varying, we want the estimation of a_i' based only on the first observations and these b_i' values. To do so, we use arbitrarily the first 5 years $y_{i,1:5}$ and $S_{i,1:5}$ to compute $a_{i,1:5}'$ by solving the following equation:

$$a'_{i,1:5} = y_{i,1:5} - b'_{i} \cdot S_{i,1:5}$$

The mean of the five values $a'_{i,1:5}$ is used for the mean of the $a_{i,0}$ prior. To limit the sensitivity of parameter estimates to this value of the first estimates of a, we set the prior with a very large variance (10⁵).

The error terms are estimated by maximization of the likelihood within the DLM package (Petris et al. 2009) in the statistical software R. Starting values for the standard deviations correspond to guesses based on the observation likelihood surface (Fig. S1¹).

Monotonic directional drift and external drivers of productivity

If a productivity time series is different from simple white noise, it might be relevant to test if it can be better described with a monotonous trend described by a drift term, as well as test its relationship to potential climate drivers. Including such external drivers aims to better predict the productivity evolution. A stock-by-stock varying model is used as a baseline for this type of model; for brevity we use the term environment-driven models to refer to models with either a drift term or climate variable included. The process model (eq. 3) is rewritten as

(6)
$$a_{i,t} = a_{i,t-1} + c_{i,j} \cdot Z_{j,t-lag} + w_{i,t}$$
 with $w_{i,t} \sim N(0, \sigma_{w_i}^2)$

where $c_{i,j}$, is a constant parameter referring to the stock i and the covariate j and $Z_{j,t-\text{lag}}$, the covariate j at year t-lag; the lag is set given literature information (Table 2). For the simple drift formulation describing a monotonous trend in productivity, $Z_{j,t-\text{lag}}$ is set to 1.

Productivity covariance among the stocks

Accounting for productivity covariance among the stocks could lead to more accurate estimates (Minto et al. 2014). Moreover, with a well-developed covariance matrix, stocks with longer time series could be used to estimate the productivity of stocks with truncated time series of recruitment and SSB or stocks with uncertain terminal years. The corresponding model with a full time-covarying productivity (called full-covarying model) is described. It is the same as the varying model with the same snr, but a different variance–covariance submatrix \mathbf{W}_a :

$$(7) \qquad \mathbf{W}_{a} = \begin{bmatrix} \sigma_{w_{1}}^{2} & \operatorname{cov}_{w_{1},w_{2}} & \dots & \operatorname{cov}_{w_{1},w_{l}} \\ \operatorname{cov}_{w_{2},w_{1}} & \sigma_{w_{2}}^{2} & \dots & \operatorname{cov}_{w_{2},w_{l}} \\ \vdots & \vdots & \ddots & \vdots \\ \operatorname{cov}_{w_{l},w_{1}} & \operatorname{cov}_{w_{l},w_{2}} & \dots & \sigma_{w_{l}}^{2} \end{bmatrix}$$

This last model contains a large number of covariance parameters $(I \times (I - 1)/2)$, with I being the stock number); however, many of them may not be significantly different from zero.

A second model is developed to optimize the number of covariance parameters to account for noninformative parameters (called partial-covarying model). Testing all partial time-covarying possibilities (2^{I-(I-1)/2}) is not reasonable and would be far too time-consuming. To minimize the number of models to be tested an iterative method, we started with the full covariance model. Initially, the absolute values of the correlation matrix elements defined in the full time-covarying model are calculated. The covariance parameter corresponding to the lowest correlation

value is set to 0 and the new model is estimated. This operation is done iteratively. The last model corresponds to all covariance parameters set to 0 (i.e., the varying model). For computing capacity reasons, these models were developed separately for the three species groups (pelagic, demersal, and flatfish), but can be potentially extended for any pool of stocks.

Model output analyses

Time consistency of productivity

Considering time-varying productivity is relevant if productivity differs from simple white noise around the mean. For each stock, we calculate the difference between the productivity time series of the varying model and the average productivity. We then calculate the length of positive runs and negative runs over each stock's time series (number of years that this difference is consecutively of the same sign) and calculate the average length of positive or negative runs for each stock. The greater this number, the further the time series is from white noise and, consequently, the more the time-varying productivity should be considered as relevant.

Main productivity pattern among the stocks

In an attempt to understand the main trend of the time-varying productivity terms across all the stocks, we employed dynamic factor analysis (DFA) with a single trend (Zuur et al. 2003). The main trend tendency among the productivity time series would synthesize the patterns of fish productivity over the Northeast US continental shelf. The balance between positively and negatively related stocks to this trend would reveal the most consistent pattern of fish productivity in this ecosystem. The power of this trend to explain the productivity variability among the fish stocks would indicate the consistency or the inconsistency of the productivity evolution among the stocks. All scaled productivity time series from the varying model are used as observations. DFA is described here in matrix form:

(8)
$$\mathbf{Z}_t = Hp_t + m_t \text{ with } v_t \sim N(0, M)$$

(9)
$$p_t = p_{t-1} + n_t \text{ with } w \sim N(0, \sigma_n^2)$$

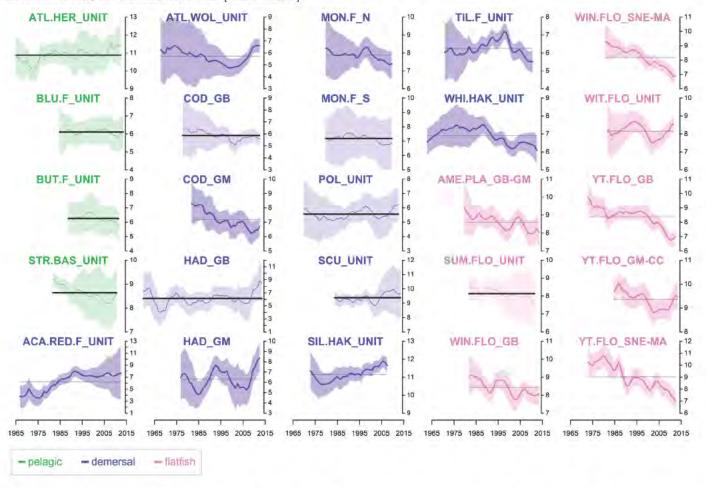
Matrix $\mathbf{Z}_t = (z_{1_t}, z_{2_t}, ..., z_{I_t})'$, with z_{i_t} the scaled productivity for the ith stock at time t, $H = (c_1, c_2, ..., c_l)'$, with c_i the correlation coefficient to the trend for the ith stock. Matrix $\mathbf{M} = \mathrm{diag}(\sigma_{m_1}^2, \sigma_{m_2}^2, ..., \sigma_{m_l}^2)$. Vector \mathbf{p}_t is the productivity trend at time t; the time series is initialized with the prior $p_0 \sim \mathrm{N}(0, 10^5)$.

Model comparison

Selecting the best baseline models (invariant versus varying models) and comparing the best baseline models with the environment-driven models is done stock by stock with the common signal-to-noise ratio. These steps are based on two different indices: a likelihood-ratio test and the gain of forecast accuracy, which provide different but complementary sources of information. The likelihood-ratio test is a χ^2 test with the corresponding difference of degrees of freedom between the two models. From the time-invariant to the time-varying models, one degree of freedom is removed due to the addition of estimating the variance of the time-varying parameter. From the time-invariant to the environment-driven models, two degrees of freedom are removed (one for the estimation of the variance of the time-varying parameter and one for the estimation of the drift or the regression parameter). From the time-varying to the environment-driven models, one degree of freedom is removed (drift or regression parameter). The likelihood ratio test uses the full time series.

The forecast-accuracy gain is based on the ability of the models to forecast future observations using truncated time series. The number of time steps into the future is denoted as d (from 1 to 3).

Fig. 3. Average (in black) and time-varying (in color) productivity time series for each stock; refer to Table 1 for stock abbreviations. The 95% confidence interval is displayed for the varying model. When the invariant model is the best baseline model, invariant productivity is brightened and time-varying productivity is shaded, and reciprocally when the varying model is the best. Acadian redfish data have been shortened to 1967; see Discussion for details. [Colour online.]



In the baseline case, starting from time t = T - 15, T being the terminal year of the available time series, we compute the log(R/ S)_{t+d} forecasts from the time-invariant model and the time-varying model; we then separately compare these forecasts with the observed value at time t + d. For the environment-driven model comparison, starting from time t = T - 15, we compute the log(R) S_{t+d} forecasts from the baseline model (determined previously) and the driven model using observed covariates; we then separately compare these forecasts with the observed value at time t +d. In both cases, the residuals are simply the difference between the model-predicted forecast and the observed value. The gain of forecast accuracy at a horizon d years is then defined as the ratio of the difference between the residual variances of the null model and the alternative model to the residual variance of the null model:

$$\operatorname{gain}_{d} = \frac{\sum_{t=T-15}^{T-d} (F_{t+d|t,\text{null}} - Y_{t+d,\text{obs}})^{2} - \sum_{t=T-15}^{T-d} (F_{t+d|t,\text{alt}} - Y_{t+d,\text{obs}})^{2}}{\sum_{t=T-15}^{T-d} (F_{t+d|t,\text{null}} - Y_{t+d,\text{obs}})^{2}}$$

The forecast at time t + d given information to time t is $F_{t+d|t}$, with either the null or alternative model; the observation of log(R/S) at time t + d is $Y_{t+d,obs}$.

Owing to large confidence intervals in the early part of the time series, the gain of forecast accuracy test was only performed on the last 15 years of observations. If there is a strong trend or a

relationship between the productivity term and an environmental covariate over the length of the time series, the likelihood ratio test would indicate that the environment-driven model is the better model. If the drift term or the environmental covariate improves the 1-to-d-year forecast into the future starting from the current value, the gain of forecast accuracy test would also indicate that the environment-driven model is a better model. Inconsistencies between the likelihood-ratio test and the forecast-accuracy gain would suggest there is an inconsistency between the potential driver of the long-term pattern and the ability to use that driver to forecast 1 to d years into the future. In an attempt to understand the potential benefit of including environmental drivers, we considered the future environmental drivers (1 to d years in the future) fully known. While the future values of environmental drivers cannot be fully known, this assumption was incorporated to understand the maximum potential gain that could be derived with environmental drivers.

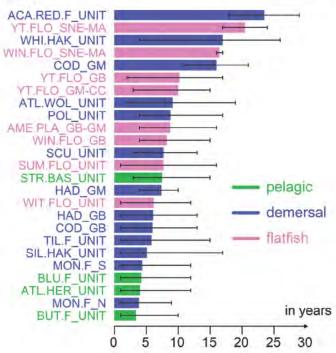
Comparison between the varying model and all covarying models is done at the multistock scale with the corrected Akaike information criterion (AIC_c).

Results

Patterns in time-varying productivity

The amplitudes of the time-varying productivity vary from less than 1 (e.g., the bluefish (Pomatomus saltatrix) stock) to around 5 (e.g., the Acadian redfish (Sebastes fasciatus) stock; Fig. 3). This vari- F3

Fig. 4. Average number of years that the varying productivity is consistently above or below the time-invariant productivity value for each stock (see Materials and methods for a detailed explanation). The black intervals represent the minimum and maximum number of years above or below the mean observed along the time series. [Colour online.]

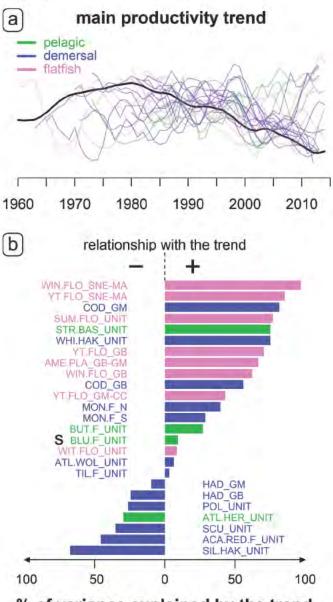


ability is huge as it corresponds to the recruit number per metric ton of the SSB on a logarithmic scale. Productivity time series are quite heterogeneous among the stocks but are different from white noise for 15 of the 25 stocks (Fig. 3). For the pelagic stocks, the productivity is quite stable over time, whereas it is decreasing for the majority of the flatfish stocks. There is a large diversity of patterns for the demersal stocks, but the productivity is constant over time for only 5 of 13 demersal stocks. The average confidence interval can be very different from one stock to another. In the terminal year, the varying productivity is below the average productivity for 14 of the 25 fish stocks. The estimated signal-to-noise ratio is 0.75.

Across all stocks, the mean length of time that the productivity is above or below the time-invariant productivity value was 9.1 years (Fig. 4). This consistency varies greatly among the stocks (from 3.4 years to 23.5 years). For five stocks, the consistency reaches at least 16 years. To generate a test statistic for the average run length, we simulated observed "productivity" time series using random walks with white noise distributed error. Productivity was then estimated from the simulated time series with the Kalman filter; the average duration of positive and negative runs under the white noise hypothesis was 2 years. These results suggest that the varying productivity is far different from white noise and supports the idea that the average productivity hypothesis is rejected for most of the stocks.

The main variability pattern of the productivity time series for all stocks was calculated from a single-trend DFA (Fig. 5). The trend corresponds to a time series decreasing consistently from the 1980s, which is a time period when almost all stocks started to be assessed. The productivity of each stock can be either positively or negatively related to the overall trend. The trend explains 46% of the overall productivity variability, but varies from 3% to 97% among the stocks. The range of variability accounted for by the trend underlines the diversity of the productivity patterns among

Fig. 5. (a) Main trend (in black) explaining the maximum amount of variance among the productivity time series of all stocks (in various colors). (b) Percentage of variance explained by this main trend; stocks positively related to the trend are to the right of the midline; negatively related ones are to the left. [Colour online.]



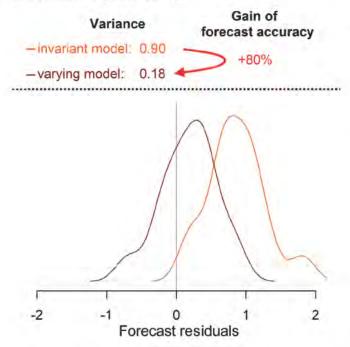
% of variance explained by the trend

the stocks. For a majority of the stocks (72%), the productivity is positively related to this trend, suggesting that a decline in productivity is the main trend among the fish stocks of the Northeast US continental shelf. All flatfish stocks are positively related to the main trend. The positive relationships are also of a greater magnitude than the negative ones.

Comparison between time-varying and invariant models

The gain of forecast accuracy of the time-varying model over the time-invariant model is illustrated by southern New England – mid-Atlantic winter flounder (Fig. 6; detailed results in Table S2¹). In this example, both models consistently overpredict the productivity over the last 15 years, but the overprediction is far greater for the invariant model. Consequently, the residual forecast vari-

Fig. 6. Density distribution of the 1-year forecast residuals for the baseline models. The example of the southern New England – mid-Atlantic winter flounder is illustrated here. Only the last 15 years are used. A forecast residual is the difference between the forecast of the $\log(R/S)$ given all observations to the year t-1 (t-d for a d-year forecast) and the observation of $\log(R/S)$ in year t. The gain of forecast accuracy of the varying model over the invariant model is measured by the relative decrease of the forecast residual variance between the two models (e.g., 10). In this example, the residual variances of the invariant model and the varying model are 0.90 and 0.18, respectively. The gain of forecast accuracy in using the varying model is thus 80%. [Colour online.]



ance is lower for the varying model, and the gain of forecast accuracy is positive (+80%).

Figure 7 presents the likelihood ratio tests and the gain of forecast accuracy from 1-year to 3-year forecasts for all stocks. At a 1-year forecast, 80% of the stocks are better predicted with the varying model. At a 2-year forecast, it decreases to 64%, and at a 3-year forecast, it is 48%. For subsequent years, this value is never under 40% (tested up to the 10-year forecast). For 60% of the stocks, the likelihood-ratio test is significant, which means that the varying model fits the observations better. The gain of the 1-year forecast accuracy is always positive for these stocks, representing a considerable improvement in short-term forecasting (+53% on average). It is interesting to note that some stocks, better described with an invariant model, also have a positive gain at the 1-year forecast with the varying model. At the 2-year forecast, some stocks better described with the varying model have a loss. This pattern increases with the forecast, meaning the further into the future the model predicts, the worse the varying model performs. The invariant model is always better for the pelagic stocks, whereas the varying model generally performs better for the flatfish and demersal stocks.

Models with trends and environmental covariates

Environment-driven models are compared with the best baseline model for each stock (either the invariant or the varying model; Fig. 8; detailed results over 3-year forecasts can be seen in Table S3¹). The drift is only significant for southern New England – mid-Atlantic winter flounder and weakly significant for Gulf of Maine cod and Georges Bank yellowtail flounder. For all of them, the drift is negative (cf. Fig. 3). The gain of forecast accuracy is important in each case and increases with the number of years projected into the future. This last point is intuitive and supports the interest of using the drift for long-term projection for such stocks. The sea surface temperature (SST)-driven model is weakly significant for eight stocks, and it is associated with a loss of forecast accuracy for five of them. The significance means that there is a significant relationship between the full time series of time-varying productivity and the full time series of SST. The loss in forecast accuracy indicates that including SST in the model to predict 1 or more years into the future from the current year results in forecasts that are worse than not using SST. The inconsistency between these two indicators suggests that there may be an overall, long-term relationship, but for predicting next year, SST is not useful. It could also suggest that the relationship between productivity and SST weakens over the last 15 years (i.e., the forecast gain was only tested over the last 15 years). SST was significant and improved the forecast for three stocks, however: Acadian redfish, southern New England - Mid Atlantic winter flounder, and southern New England - Mid Atlantic yellowtail flounder. The NAO is insignificant except for the white hake (Urophycis tenuis) stock. The cold pool has been related to the carrying capacity of southern New England - mid-Atlantic yellowtail flounder (Miller et al. 2016), but the relationship was not apparent in this study. Results for the cold pool are not shown, as there was no relationship with southern New England stocks. The Gulf Stream North Wall appears to be a potential driver for a few stocks. In general, the potential drivers improve the predictions of productivity for only a few stocks. This is in accordance with the diversity of productivity patterns observed among the stocks, suggesting that a single broad-scale signal was not detected as a driver for the majority of the stocks (Fig. 3).

Comparison between varying models and covarying models

Based on the corrected Akaike criterion, the varying model is always better than the full-covarying model for all three fish categories (Table 3). The best partial-covarying model contains between 0% and 28% of the covariance parameters of the fullcovarying models. This suggests that the productivity differs greatly among the stocks on the Northeast US continental shelf. Of the terms that remain in the model, the correlation matrix of the best partial-covarying models displays mostly positive correlation coefficients (Fig. 9). The correlation is always strong and positive between the two stocks of the same species located in two adjacent areas: Gulf of Maine and Georges Bank (cod, haddock (Melanogrammus aeglefinus), yellowtail flounder). This suggests that the productivity variations are driven by connected processes in these areas. The correlation between the demersal stocks is sometimes strong (close to 1 or -1), meaning that the productivity of a stock is also widely informed by the related stocks.

Discussion

This study advances the methodology for fitting dynamic linear models to stock–recruitment data from multiple stocks. The assumption of a common signal-to-noise ratio allows information to be pooled among stocks, resulting in more robust estimates of time-varying parameters. We also demonstrate that monotonic trends and environmental covariates can be introduced directly into the Kalman filter as opposed to testing their effects post hoc (Collie et al. 2012; Britten et al. 2016).

Through a multispecies approach at the scale of a large ecosystem, we show that a large number of fish stocks exhibit changes in maximum reproductive rate over time. These results agree with previous work at the single-stock scale(Miller et al. 2016; Bell et al. 2018; Xu et al. 2018) and at a single-species scale (Peterman et al. 2003; Dorner et al. 2008; Minto et al. 2014). This study demonstrates that the recruitment is better predicted for a large number of fish stocks by accounting for dynamic productivity, which is of

Fig. 7. Gain of forecast accuracy of the varying productivity model over the invariant model at three different lags (1 to 3 years). A likelihood ratio test (χ^2 test with one degree of freedom, corresponding to the additional process-error parameter to estimate in the varying model) is done to conclude whether the varying model is more relevant. Significant test results are indicated (P values: *, <0.05; **, <0.01; ***, <0.001). [Colour online.]

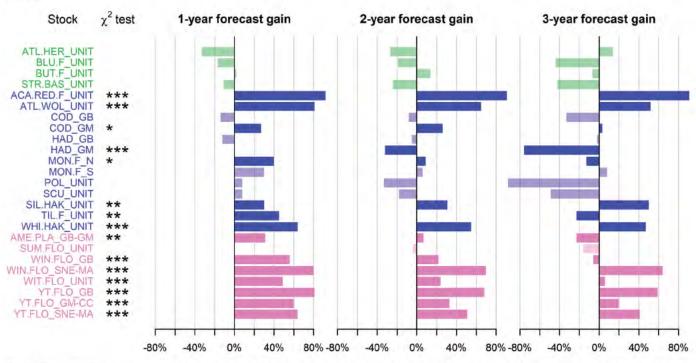
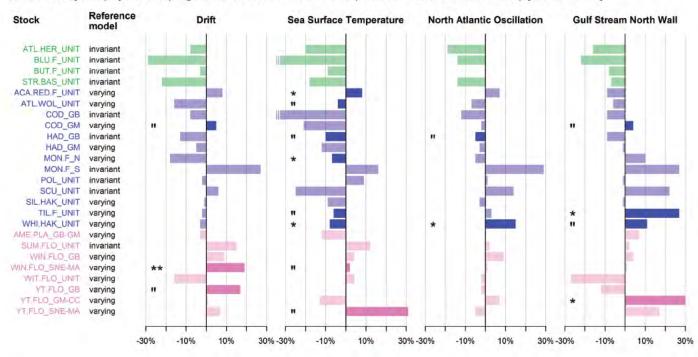


Fig. 8. Gain of forecast accuracy of the environment-driven models at 1-year horizon (reference model is the best between the invariant and the varying models). This gain is based on the last 15 years. A likelihood-ratio test is done to conclude if the environment-driven model is more relevant (2 degrees of freedom if the reference model is the invariant one, 1 if it is the varying model). When a negative forecast gain is associated with a significant test, it means that the relationship is strong on average over the entire time series, but is not any more relevant on the recent years (15 years here). Significant test results are indicated (*P* values: ", <0.01; *, <0.05; **, <0.01). [Colour online.]



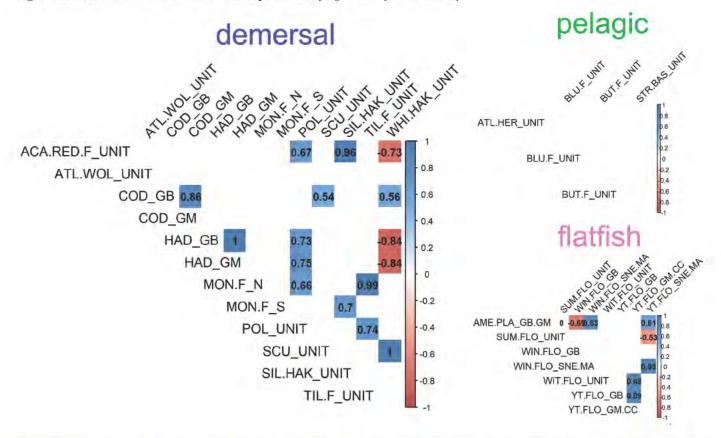
central importance for fisheries management. For a few stocks, recruitment can be better predicted by including simple environmental covariates or covariance among the stocks, but this study demonstrates the challenges of making these links and including

them in management. Currently, mechanistic links between environmental drivers and intrinsic rates or processes are rarely strong enough or simple enough to use in assessments, and they can change over time as different drivers change in their level of

Table 3. Comparison between the fits of the varying model and the covarying models.

Fish community	Model value	Varying model	Full-covarying model	Best partial-covarying model
Pelagic (4 stocks)	No. of covariance parameters	0	6	0
	AIC _c value	190.4	199.3	190.4
Demersal (13 stocks)	No. of covariance parameters	0	78	16
	AIC _c value	478.8	562.8	442.3
Flatfish (8 stocks)	No. of covariance parameters	0	28	8
	AIC _c value	262.1	278.9	241.4

Fig. 9. Partial correlation matrices from the best partial-covarying models. [Colour online.]



importance (Myers 1998; King et al. 2015; Skern-Mauritzen et al. 2016). In the absence of mechanistic links, it is still possible to estimate changes in productivity and to use these estimates to make short-term projections.

Patterns in productivity

In this study, we assume a common signal-to-noise ratio across all the stocks on the Northeast US shelf because the observation time series are generally too short to robustly disentangle the observation error from the process error stock by stock. Using state-space models, especially in an ecological study, can suffer from the challenges of parameter estimation (Auger-Méthé et al. 2016). By assuming that the signal-to-noise ratio is shared among the stocks, we decrease that risk by informing the partitioning between the error parameters with a large data set. This technique advances the methodology and avoids the unrealistic result of models with a null observation-error term. Sensitivity runs show that the common signal-to-noise ratio enables estimates that fall within an acceptable optimization surface, since the estimation surface is very flat at its maximum. The estimated signalto-noise ratio falls in the range of similar studies (Peterman et al. 2003; Minto et al. 2014). As the ratio is smaller than 1, most of the noise corresponds to errors in the observations, which is expected

as they correspond to model outputs and contain uncertainties by definition. Other studies have addressed this issue by fixing the signal-to-noise ratio (de Valpine and Hilborn 2005) or with a prior centered on 1 (Pedersen and Berg 2017). Here we are able to use the data itself to estimate the common signal-to-noise ratio. Longer observation time series in the future could potentially remove the need for the common signal-to-noise ratio among stocks, but testing the sensitivity of the error estimations remains essential.

While this work improves on previous studies and expands the method, challenges remain. We recognize that the input into the state-space model is the output from a stock assessment model. The assessment models integrate information from several sources to provide the best estimates of SSB and recruitment currently available. The dynamic linear models account for estimation error in the inputs via the **observation** residuals (v_t). Within the observation model, the SSB is on both sides of the Ricker equation and contains estimation error. A positive error in SSB would lead to underestimated observations in the equation, but the negative density-dependent effect partially compensates for this error (depending on the strength of this density-dependent effect), and consequently, the error of the SSB has a limited effect on the estimation of the maximum reproduction rate. While many of the

assessment models also contain stock-recruitment functions that could influence the productivity results, in general, the objective functions of the assessment models are configured such that the stock-recruitment functions have little influence over the estimates of recruitment. The coefficient of variation for recruitment is typically quite large, ensuring that the catch-at-age data from the fisheries-independent and -dependent sources drive recruitment. The method is self-checking, in that if a stock-recruitment function were used to estimate recruitment, the state-space model would estimate a relatively smooth, time-invariant productivity term. Several of the fish stocks used in this study exhibit retrospective patterns, whereby estimates of R and S for a recent year change retrospectively as new years of data are added to the analysis (Mohn 1999). Retrospective patterns will also occur in the productivity estimates, though they are damped somewhat in the ratio R/S, because R and S usually change in the same direction. The time-varying productivity estimates do not correct for potential retrospective patterns, but are also not the result of retrospective patterns because strong variations are observed all along the time series, not only in the final years.

The time-varying state-space model provides a better description of the productivity for a number of stocks. The trend describing the best productivity time series across all stocks corresponds to a consistent decrease in productivity since the 1980s. This consistent decrease suggests that the Northeast US continental shelf ecosystem is undergoing a long-term change in the dynamics of its fish communities. More stocks were positively related to the trend, potentially suggesting a shift to an ecosystem more dependent on fewer stocks with higher productivity. However, this general pattern hides a more complex situation with a large diversity of trends among the stocks. While the single trend from the DFA captures much of the variance for some stocks, it accounts for only a small fraction for others, and the trend has a negative relationship for some stocks. Similarly, there are relatively few terms in the partial-covariance matrices, indicating that there are not many common patterns across the stocks. The productivity of demersal stocks exhibits a large range of patterns, both positive and negative, while the pelagic fish are best described by timeinvariant models; the flatfish stocks generally exhibit a decline in productivity as has been seen in other studies (Bell et al. 2014). While other studies have found evidence of regime shifts on the Northeast US shelf (Perretti et al. 2017), it was not present in the DFA trend. Collie et al. (2008) found that fish composition had shifted from a demersal-dominant community to a pelagicdominant community in a coastal bay within the Northeast US shelf. We found declines in productivity for a number of bottomoriented stocks, but not a subsequent increase in productivity for pelagic species that could lead to an increase in abundance and shift in the pelagic-demersal ratio on the basis of recruitment

There are two main mechanisms leading to an increase in productivity. First, the spawners can be more fecund through such processes as improved condition factor heading into the spawning season (Leaf and Friedland 2014) or an expanded age structure with more older and larger individuals that produce more viable eggs than young mature fish (Hutchings and Myers 1993). Second, the proportion of individuals reaching recruitment increases. There are a range of biological mechanisms associated with increased survival during the earliest life stages, such as advection to nursery grounds (Garvine et al. 1997), suitable physiological conditions, reduced predation (van der Veer et al. 2000; Taylor and Collie 2003), and sufficient food (Castonguay et al. 2008). Broadscale environmental changes can affect the whole ecosystem (Klein et al. 2017), altering oceanographic and energetic pathways, which in turn impact stock productivity.

This study found relatively few relationships between environmental drivers and stock productivity. Strong patterns across numerous stocks were not apparent in any of the analyses, suggesting that broad-scale environmental covariates may not provide simple, straightforward understanding of stock dynamics. Even the use of perfect predictions of environmental covariates provided a gain in forecast accuracy for only four of the 25 stocks. This is not to say that the environment is unimportant, but only that the exact mechanism may not have been identified. For instance, only a linear relationship was tested between SST and productivity even though a hypothesis considering an optimum temperature window, but requiring more parameters, is more likely (Jobling 1994; Mantzouni et al. 2010). The optimum temperature window hypothesis might help explain the discrepancy in the relationship between SST and productivity for the five stocks that were significant, but forecasts were not improved with SST. The temperature in the most recent years is warmer and outside the range of temperatures in the majority of the SST time series. This example emphasizes the importance of using complementary tools to check the consistency of a relationship over time and cautions forecasting based on an extrapolated relationship. The results, however, do support some previous studies relating stock productivity with environmental covariates such as southern New England - Mid Atlantic winter flounder (Jeffries and Johnson 1974; Bell et al. 2014).

The broad productivity patterns among the fish species suggest that they are affected by different covariates or at least by different mechanisms related to common covariates. The few correlations with climate covariates are consistent with these conclusions. The positive covariance among the same species, but different stocks, in the Gulf of Maine and George Bank is consistent with other recent observations (Dorner et al. 2008; Minto et al. 2014) and supports the hypothesis that there are regional drivers affecting several stocks at the same time (Rothschild 2007). The lack of environmental relationships that hold up over time underscores three important concepts: (i) demonstrating robust links between population dynamics and the environment is both challenging and time consuming; (ii) the state-space method used here can detect and account for changes in productivity without understanding the underlying mechanism; and (iii) the state-space method can rapidly examine stocks for changes in productivity and be used to focus climate research on those stocks with the most to gain.

Management implications

Two main components lead to variations in exploited fish stock dynamics: the evolution of the adult stock size and the ability of the fish to produce recruits (i.e., productivity). The variation of predation and (or) fishing pressure on the adult fish stock can be directly quantified by accounting for the predator abundance within a multistock model and (or) the measurement of the fishing pressure (Quinn and Deriso 1999). Variations in productivity are not directly observable, but the state-space approach used here shows that different tools can be used to anticipate productivity evolution and thus provide valuable information for management.

One of the main tasks of management is to set harvest levels for upcoming fishing seasons, which involves projecting SSB and recruitment levels 1–3 years in the future. This study focused on recruitment projections, recognizing that considerable error also exists in SSB forecasts (Wiedenmann and Jensen 2018). The simple varying productivity models provided good forecast power in the short term (1–3 years) for most species and generally outperformed the time-invariant models. The multispecies inference using the covariance matrix (Minto et al. 2014) is an effective technique to improve recent productivity estimates and thus forecasts, particularly for stocks with limited information. However, it was not overly applicable to stocks on the Northeast US shelf. Owing to the lack of broad productivity patterns, there was relatively little information in the covariance matrix, limiting its use in the region. Likewise, the lack of many strong environmental

relationships limited their ability to improve short-term forecasts. Should new environmental relationships come to light, the machinery is prebuilt within the state-space models and could be easily incorporated.

The varying-productivity models may improve current practices that forecast biomass with the most recent information such as recruitment and weight-at-age over the last few years. While forecasting is important, the utility of the dynamic productivity term goes beyond biomass forecasting and is able to directly inform sustainable harvest practices (Collie et al. 2012). Reference points are a direct function of productivity. If productivity is changing, the exploitation level that a stock can sustain is also changing, suggesting that dynamic reference points may be useful. While major changes in reference points and catch levels on an annual basis would be untenable, well-crafted, dynamic reference points could enable adaptable management practices that are more in tune with the current state of the ecosystem.

While strong environmental drivers did not emerge for the majority of the stocks, the demonstration of time-varying productivity for a large number of stocks on the Northeast US shelf provides valuable information for future management. Regardless of the drivers, harvest control rules that incorporate dynamic productivity could benefit the provision of catch advice for fisheries management on the Northeast US shelf.

Acknowledgements

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