

Productivity dynamics of Atlantic cod

Cóilín Minto, Joanna Mills Flemming, Gregory Lee Britten, and Boris Worm

Abstract: Productivity is a central determinant of population dynamics with consequences for population viability, resilience to exploitation, and extinction. In fish, the strength of a cohort is typically established during early life stages. Traditional approaches to measuring productivity do not allow for interannual variation in the maximum reproductive rate, a parameter governing population productivity. Allowing such process variation provides the ability to track dynamic changes instead of assuming a static productivity regime. Here we develop and evaluate a multivariate stock–recruitment state-space model to simultaneously estimate time-varying stock productivity and synchronicity of dynamics across populations. We apply the method to North Atlantic cod (*Gadus morhua*) populations, showing that the productivity of early life stages has varied markedly over time, with many populations at historically low productivity. Trends in productivity were similar in some adjacent populations but less regionally coherent than previously thought, particularly in the Northwest Atlantic. Latitudinal variation in the Northeast Atlantic suggests a differential response to environmental change. We conclude that time-varying productivity provides a useful framework that integrates across many dimensions of environmental change affecting early life history dynamics.

Résumé : La productivité est un déterminant central de la dynamique des populations, qui a des répercussions sur la viabilité de la population, la résilience à l'exploitation et la disparition. Chez les poissons, la force d'une cohorte s'établit typiquement durant les premiers stades du cycle de vie. Les approches traditionnelles de mesure de la productivité ne permettent pas de variations interannuelles du taux de reproduction maximum, un paramètre qui régit la productivité de la population. En permettant de telles variations, il devient possible de suivre les changements dynamiques plutôt que de présumer que le régime de productivité est statique. Nous avons mis au point un modèle d'espace d'états de la relation stock–recrutement afin d'estimer simultanément la productivité variable dans le temps des stocks et le synchronisme de la dynamique de différentes populations. Nous avons appliqué cette méthode aux populations de morues de l'Atlantique Nord et démontré une variabilité marquée de la productivité des premiers stades du cycle de vie dans le temps, la productivité de nombreuses populations en étant actuellement à un creux historique. Les tendances en matière de productivité étaient semblables pour certaines populations voisines, mais moins cohérentes que prévu à l'échelle régionale, particulièrement en ce qui concerne le nord-ouest de l'Atlantique. Les variations latitudinales dans le nord-est de l'océan Atlantique semblent indiquer des variations dans l'espace en ce qui concerne les réactions aux perturbations environnementales. Nous concluons que la productivité variable dans le temps constitue un cadre utile qui fournit une représentation intégrée sur plusieurs dimensions des modifications du milieu qui ont une incidence sur la dynamique des premiers stades du cycle de vie. [Traduit par la Rédaction]

Introduction

During their early life history, fish are most vulnerable to competition, predation, hydrography, temperature, and a host of other environmental factors that result in extraordinarily high levels of natural mortality (Harding and Talbot 1973; Cushing 1975). The varying ability to survive and grow through the early stages ultimately determines how many fish will recruit to the adult population and enter a fishery. Understanding the dynamics of this period is therefore critical to understanding fish population dynamics and the management of fisheries resources (Allen 1963; Cushing 1975; Mace and Sissenwine 1993). Despite a century of fruitful investigation, however, much uncertainty remains in our understanding of stock replenishment (Myers 1998, 2001; Houde 2008).

Hypothesized processes affecting the strength of a recruiting year-class or cohort are manifold, including spawner abundance and composition (Trippel et al. 1997; Marshall et al. 2006; Green 2008), density-dependent and density-independent mortality via

predation, competition, the physical environment, and the many interactions therein (Houde 2008; Green 2008). While investigations of particular agents or indicators of mortality (e.g., temperature anomalies, North Atlantic Oscillation, abundance of predators and competitors) can yield useful insights (Worm and Myers 2003; Brander and Mohn 2004; Minto and Worm 2012), other candidate hypotheses are often excluded. For example, while the focus on relating the strength of recruitment to the physical environment (Planque and Frédou 1999; Brander and Mohn 2004; Mantzouni et al. 2010; Mantzouni and MacKenzie 2010) is of intrinsic importance, such investigations often exclude other factors such as maternal effects (Trippel et al. 1997; Marshall et al. 2006; Lambert 2008), predation or competition (Minto and Worm 2012), resource availability and phenology (Kristiansen et al. 2011). In an extreme case, there can exist more candidate hypotheses than yearly abundance observations from constituent populations, for example, explaining at-sea survival of Atlantic salmon (*Salmo salar*) (Cairns 2001).

Received 15 March 2013. Accepted 26 September 2013.

Paper handled by Associate Editor Kenneth Rose.

C. Minto. Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland.

J. Mills Flemming. Department of Mathematics and Statistics, Dalhousie University, Halifax, NS B3H 4R2, Canada.

G.L. Britten and B. Worm. Biology Department, Dalhousie University, Halifax, NS B3H 4R2, Canada.

Corresponding author: C. Minto (e-mail: coilin.minto@gmit.ie).

Rather than pose a specific hypothesis as a proximate agent of prerecruit productivity, we focus on the question of whether prerecruit productivity of Atlantic cod (*Gadus morhua*) has changed over time and, where observed, whether such changes are conserved across populations. This simple question has received remarkably little attention, with some notable exceptions (Zeng et al. 1998; Peterman et al. 2003; Dorner et al. 2008).

Previous investigations on the covariance of recruitment across populations serve as a basis for the investigation. By accounting for the effect of spawner abundance on recruitment and detrending the resultant residuals, Myers et al. (1995b) discovered that the spatial scale (measured as mean e-folding distance of pairwise correlations) of cod recruitment is approximately 500 km, a result confirmed in a similar pan-species investigation by Myers et al. (1997). Rothschild (2007) concluded that recruitment of cod covaried across 11 populations in the Northwest Atlantic. It is unclear, however, the degree to which this covariance reflects changes in the adult spawner biomass (Cardinale and Hjelm 2006) and thus common trends in fishing mortality, inferred common environmental forcing, or both. Kelly et al. (2009) showed that the synchrony of recruitment of cod stocks in the Northwest Atlantic has declined over time. While of importance to indicating the degree to which a response is common among populations, correlative studies are somewhat removed from population dynamics and therefore difficult to incorporate into management advice.

Peterman et al. (2003) and Dorner et al. (2008) presented foundational univariate (single population) state-space methods to extract filtered and smoothed time-series trends in productivity for multiple species and populations of Pacific salmonids. A population dynamics model was specified in which parameters were allowed to vary over time according to stochastic processes. Importantly, allowing the parameters to vary over time permits the separation of process variation in the parameters from measurement error in survival. Peterman et al. (2003) thus found that the productivity of sockeye salmon (*Oncorhynchus nerka*) had changed markedly over time, with interpopulation changes shown to be more tightly conserved when using a time-varying population dynamics model than that obtained with a correlative approach. Of considerable applied importance is that by choosing to formulate a time-varying population dynamics model, the effect on resource management could be explored thoroughly (Collie et al. 2012).

Peterman et al. (2003) and Dorner et al. (2008) estimated the correlation between population-specific (univariate) time-varying trends in productivity after fitting the state-space model via correlation of the smoothed states. Here we extend this method to a multivariate time-varying population dynamics model that simultaneously estimates trends in productivity and the covariance therein across populations. We apply the method to 11 Northeast and 10 Northwest Atlantic cod populations to (i) test whether the population dynamics have changed over time; (ii) determine the spatial coherence of productivity; and (iii) interpret the scale of population dynamics changes where they exist. The applied impetus lies in the need for scientific understanding and management reflecting present productivity conditions while making optimal use of available datasets. Our method partly addresses this requirement through the application of a novel statistical approach to recruitment studies: multivariate state-space modeling.

Materials and methods

State-space formulation

Peterman et al. (2003) provide single-population (univariate) methods for estimating time-varying productivity in stock-recruitment models. Here we extend the approach to multiple populations using a multivariate state-space model.

The traditional time-invariant parameter Ricker stock-recruitment model is written

$$(1) \quad R_{j,t} = \alpha_j S_{j,t-\tau_j} e^{-\beta_j S_{j,t-\tau_j} + \varepsilon_{j,t}}$$

where $R_{j,t}$ is the recruitment of population $j = \{1, \dots, J\}$ in year $t = \{t_{j,0}, t_{j,0} + 1, \dots, T_j\}$ (start year $t_{j,0}$ and end year T_j are stock-specific) at age τ_j ; $S_{j,t-\tau_j}$ is the spawning population biomass giving rise to the year-class; and α_j , when suitably scaled, is the maximum reproductive rate (see Data standardization below), which is the main focus of our analyses. For subsequent interpretation it is important to note that in the derivation of the Ricker model, α_j is the product of fecundity and density-independent mortality integrated over the time from spawning to recruitment (Ricker 1954), β_j is the density-dependent parameter, and $e^{\varepsilon_{j,t}}$ are log-normally distributed errors ($\varepsilon_{j,t} \sim N(0, \sigma_{\varepsilon_j}^2)$). The model can be linearized by dividing by spawner abundance and taking the natural logarithm

$$(2) \quad \ln\left(\frac{R_{j,t}}{S_{j,t-\tau_j}}\right) = a_j - \beta_j S_{j,t-\tau_j} + \varepsilon_{j,t}$$

where $a_j = \ln(\alpha_j)$. The ratio of recruits to spawners is termed survival, and we term the natural logarithm of this ratio “log survival”. The model is formulated as a time-varying regression by allowing a time dynamic on the intercept, a_j , and slope, β_j :

$$(3) \quad y_{j,t} = a_{j,t} - \beta_{j,t} S_{j,t-\tau_j} + \varepsilon_{j,t}$$

where $y_{j,t} = \ln\left(\frac{R_{j,t}}{S_{j,t-\tau_j}}\right)$. Various stochastic processes can be used to describe the time dynamic of $a_{j,t}$ and $\beta_{j,t}$, including the ARMA class (e.g., AR(1), MA(1), and ARMA(1,1)). Preliminary univariate (single-population) implementations indicated (via AIC) that the random-walk model with time-varying $a_{j,t}$ and constant β_j fit best (Minto 2011), similar to Peterman et al. (2003). We focus here on a random-walk structure for both the logarithm of the maximum reproductive rate and density dependence; e.g., for the logarithm of the maximum reproductive rate

$$(4) \quad a_{j,t} = a_{j,t-1} + \eta_{j,t}$$

where $\eta_{j,t} \sim N(0, \sigma_{\eta_j}^2)$ are termed “process errors”.

For multiple populations, it is easiest to describe the model in matrix form. The measurement and process equations are written

$$(5) \quad \mathbf{Y}_t = \mathbf{F}_t \mathbf{X}_t + \boldsymbol{\varepsilon}_t, \quad \boldsymbol{\varepsilon}_t \sim N(0, \mathbf{R})$$

$$(6) \quad \mathbf{X}_t = \mathbf{D} \mathbf{X}_{t-1} + \boldsymbol{\eta}_t, \quad \boldsymbol{\eta}_t \sim N(0, \mathbf{Q})$$

where \mathbf{Y}_t is a column vector of log survival (response) in each population for year-class t , \mathbf{F}_t is a $(p \times 2p)$ block matrix (where p is the number of stocks) with the identity as the left block and $\mathbf{S}_{t-\tau}$ on the diagonal of the right block, and \mathbf{X}_t is the state matrix with the stock-specific state vectors as its columns

$$(7) \quad \mathbf{X}_t = (a_{1,t} \ a_{2,t} \ \dots \ a_{p,t} \ \beta_1 \ \beta_2 \ \dots \ \beta_p)'$$

$\boldsymbol{\varepsilon}_t$ is a column vector of measurement errors assumed to be independently and normally distributed with a diagonal covariance matrix \mathbf{R} . Note that while $\boldsymbol{\varepsilon}_t$ are termed measurement errors, they may also contain a component of high-frequency true process error not captured in a_t . \mathbf{D} is an identity transition matrix of dimension $(2p \times 2p)$, which specifies the random walk on the parameters. In a species interactions context, Ives et al. (2003) interpreted an autocorrelated version of the transition matrix with nonzero off-diagonals as a community matrix representing

Table 1. Process covariance matrix structures investigated.

Model name	Q structure
Time-invariant	$\mathbf{Q}_a = \mathbf{0}_{p,p}$ $\mathbf{Q}_b = \mathbf{0}_{p,p}$
Time-varying productivity	$\mathbf{Q}_a = \text{diag}(\sigma_{a,1}^2, \dots, \sigma_{a,p}^2)$ $\mathbf{Q}_b = \mathbf{0}_{p,p}$
Time-varying density dependence	$\mathbf{Q}_a = \mathbf{0}_{p,p}$ $\mathbf{Q}_b = \text{diag}(\sigma_{\beta,1}^2, \dots, \sigma_{\beta,p}^2)$
Time-varying productivity and density dependence	$\mathbf{Q}_a = \text{diag}(\sigma_{a,1}^2, \dots, \sigma_{a,p}^2)$ $\mathbf{Q}_b = \text{diag}(\sigma_{\beta,1}^2, \dots, \sigma_{\beta,p}^2)$
Time-covarying productivity	$\mathbf{Q}_a = \begin{pmatrix} \sigma_{a,1}^2 & \sigma_{a_1 a_2} & \dots & \sigma_{a_1 a_p} \\ \sigma_{a_2 a_1} & \sigma_{a_2}^2 & \dots & \sigma_{a_2 a_p} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{a_p a_1} & \sigma_{a_p a_2} & \dots & \sigma_{a_p}^2 \end{pmatrix}$ $\mathbf{Q}_b = \mathbf{0}_{p,p}$

Note: A $p \times p$ matrix of zeros is denoted $\mathbf{0}_{p,p}$; “diag” denotes a diagonal matrix with zeros in the off-diagonals (i.e., time-varying with zero covariance); covariance of the maximum reproductive rate of stock i with stock j is denoted $\sigma_{a_i a_j}$.

linear relationships between the p species. We include zeroes in the off-diagonals as the populations are purportedly separated in space. $\boldsymbol{\eta}_t$ is a column vector of process errors with a multivariate normal distribution with covariance matrix \mathbf{Q} . \mathbf{Q} describes the covariance of the underlying processes across populations. The structure of \mathbf{Q} determines which parameters are time-variant or time-invariant and whether covariance of the time-varying trends is included. The general structure we implement is

$$(8) \quad \mathbf{Q} = \begin{pmatrix} \mathbf{Q}_a & \mathbf{0}_{p,p} \\ \mathbf{0}_{p,p} & \mathbf{Q}_b \end{pmatrix}$$

with the upper-left block (\mathbf{Q}_a) and lower-right block (\mathbf{Q}_b) corresponding to the covariance matrix of the time-varying maximum reproductive rates and density dependence, respectively. We investigated five models per region: time-invariant, with all parameters held constant; time-varying productivity; time-varying density dependence; time-varying productivity and density dependence; and time-covarying productivity (Table 1).

The goodness-of-fit of each model was judged by AIC, including both the number of variance parameters and the number of diffuse states initialized in the calculation of the total number of parameters (Durbin and Koopman 2001). Note that only the time-varying maximum reproductive rate was allowed to covary (Table 1), because the fit with time-varying maximum reproductive rate and density dependence was worse than that with time-varying maximum reproductive rate alone (see Results).

For the time-covarying model, where populations are behaving similarly, positive off-diagonals would be expected in \mathbf{Q}_a . Conversely, where they behave differentially, negative off-diagonals would be expected. Ecologically, the \mathbf{Q}_a matrix governs the yearly magnitude and time scale of the interannual fluctuations in productivity. An “unstructured” correlation structure, where the correlations between each pair of populations is free, was chosen here. Although this requires $p(p + 1)/2$ parameters to parameterize \mathbf{Q}_a , it makes the fewest a priori assumptions on the relationships between the populations. In total, allowing for separate measurement error variances per population and an unstructured covariance matrix for the time-varying intercepts requires $[p(p + 1)/2 + p]$ variance parameters to be estimated. We analysed the Northeast Atlantic (11 populations; 77 variance parameters) and Northwest Atlantic (10 populations; 65 variance parameters) separately.

Following estimation (see estimation section below), the covariance matrix \mathbf{Q}_a can be converted into the equivalent correlation matrix \mathbf{Q}_a for ease of interpretation via

$$(9) \quad \mathbf{Q}_a = \mathbf{D}_a^{-1} \mathbf{Q}_a \mathbf{D}_a^{-1}$$

where \mathbf{D}_a is a diagonal matrix with $\text{diag}(\mathbf{D}_a) = \sqrt{\text{diag}(\mathbf{Q}_a)}$. Following estimation, we preliminarily investigate the relationships between the off-diagonal unstructured correlations and geographic distance from the centroid of each stock using an additive model (a generalized additive model with normal errors) weighted by the number of overlapping observations per stock pair.

Filtering, smoothing, and estimation

For a given set of parameters, the Kalman filter predicts the states in the next time period, which are updated via the observations. The difference between the observations and predicted states is known as the innovation, which together with the innovation variance matrix (available analytically) form the components of the likelihood, the negative log of which is minimized over all observations to provide the maximum likelihood estimates of the parameter set. Once estimated, the parameters can be used to extract filtered states, which consider observations up to time t when predicting time $t + 1$, and smoothed states, which consider all observations before and after time t when predicting for time $t + 1$. We specify diffuse initial conditions for the multivariate Kalman filter. A full description of the Kalman filter can be found in Harvey (1991) and Petris et al. (2009).

In a multivariate setting, the start and end points of the assessment differ by population, with some stretching back close to a century, while others begin within the last 30 years. This results in ragged start and end points for the analyses. State-space models are uniquely capable of dealing with missing values by interpolating over the missing values using the transition equation only (eq. 6) during these periods (Durbin and Koopman 2001; Clark 2007; Petris et al. 2009). In the multivariate case, this provides an opportunity to estimate historical trends in productivity for a given population during a time period for which no data exist. The method relies on hindcasting using the optimized covariance matrix of the process, which is estimated in the period of overlap. The Kalman filtering and smoothing recursions and the corresponding likelihood were implemented in the R statistical environment and optimized using BFGS optimization in “optim” (R Development Core Team 2012).

For comparative purposes, we reran analyses similar to that of Myers et al. (1995b), which included obtaining population-specific residuals from a time-invariant Ricker stock-recruitment model, subsequent investigation of short- and long-term trends, and

Table 2. Summary of each population included in the analyses.

Area name	NAFO-ICES division	ID	Lat. (°N)	Long. (°W)	τ	Year-classes
Labrador-Northeast Newfoundland	2J3KL	LABNNEW	50.00	-52.00	3	1962-1998
Flemish Cap	3M	FLEM	47.00	-45.00	1	1972-2010
Southern Grand Banks	3NO	SGRAND	44.50	-51.50	3	1959-2004
Northern Gulf of St. Lawrence	3Pn4RS	NGOSL	49.00	-60.00	3	1974-2006
St. Pierre Bank	3Ps	SNEW	46.00	-55.50	3	1959-2002
Southern Gulf of St. Lawrence	4TVn	SGOSL	47.50	-63.50	3	1950-2006
Eastern Scotian Shelf	4VsW	ESS	44.00	-59.00	1	1958-2009
Southwest Scotian Shelf	4X	SWSS	43.00	-65.50	1	1948-2007
Gulf of Maine	5Y	GOM	43.50	-68.50	1	1982-2006
Georges Bank	5Z	GB	41.00	-67.00	1	1978-2006
Western Baltic	BA2224	WBAL	55.00	13.50	1	1970-2007
Central Baltic	BA2532	CBAL	56.00	19.00	2	1966-2006
Celtic Sea	VIIe-f	CS	51.00	-5.00	1	1971-2006
Faroe Plateau	Vb	FAPL	62.00	-8.00	2	1961-2004
Iceland	Va/XIVb	ICE	63.00	-21.00	3	1928-2007
Irish Sea	VIIa	IS	54.00	-5.00	0	1968-2007
Kattegat	IIIa (south)	KAT	57.00	12.00	1	1971-2007
Northeast Arctic	I, II	NEAR	68.00	15.00	3	1910-2005
North Sea	IVa-c	NS	55.00	4.00	1	1963-2007
West of Scotland	VIa	WSCOT	58.50	-6.00	1	1978-2008
Norwegian Coastal	IIa	NORCOAST	65.64	9.97	2	1984-2006

Note: Latitude and longitude refer to the centroid of the stock; τ is the age at recruitment; year-classes refer to the time span of cohorts available.

correlations of the residuals. The results of this analysis are presented in the Supplementary Material¹.

Model diagnostics

To check the assumptions of the model fit, we investigated the residuals of the best-fitting model as judged by AIC. The residuals of a state-space model are the innovations (Petris et al. 2009) or one step ahead forecast errors that are assumed to be independently and normally distributed here. We visually inspected the assumption of normality using quantile-quantile plots and tested the assumption using Shapiro-Wilks normality tests on a stock-by-stock basis. We visualized the assumption of independence by using the autocorrelation function and tested it using a Ljung-Box independence test at lag 1, again on a stock-by-stock basis. Note that the model assumes multivariate normality, whereas we assessed only marginal normality.

Data

Estimates of cod spawning population biomass and recruitment (21 regions) were extracted from a newly developed quality-controlled global fish stock assessment database (Ricard et al. 2012). Older assessment results, either from the original Myers stock-recruitment database (Myers et al. 1995a) or the literature, were spliced together with more recent assessments to create the longest possible time series (some dating to the beginning of the 20th century). Assessment methodologies were typically sequential population analyses (e.g., VPA, ADAPT) except for the west coast of Scotland cod, which was assessed using a state-space model (Fryer et al. 1998). Further details of the assessments used can be found in Minto and Worm (2012). Recent assessments were not available for some regions in the Northwest Atlantic (e.g., Northern cod (NAFO subareas 2J3KL), Southern Grand Banks (NAFO subareas 3NO), Southern Newfoundland (NAFO 3Ps). For these, we used older assessments from the collection of Shelton et al. (2006). A summary of the datasets is provided in Table 2.

Data standardization

Differences in growth rates and gear selectivity result in the age at recruitment varying by region. Myers et al. (1996) developed a method of comparing the relationships across regions by multi-

plying the recruits (in numbers) by the predicted spawner biomass per recruit, assuming zero fishing mortality ($SPR_{F=0}$) (Mace and Sissenwine 1993). This allows for the estimates of the maximum reproductive rate to be compared across populations (Myers et al. 1999). Details and a discussion of the standardization are provided in Minto and Worm (2012).

Results

Trends in survival

Exploratory plots of cod log survival (after removing the effect of spawner abundance; see Supplementary Material¹) provide an overview of the data (Fig. 1). Some populations have marked patterns in the residuals, particularly the Northwest Atlantic populations (e.g., Flemish Cap, Southern Grand Banks, and Labrador-Northern Newfoundland populations). Population pairs such as the Celtic Sea and Irish Sea and Gulf of Maine and Georges Bank share strongly covarying patterns in the residuals, whereas other adjacent populations have contrasting residual patterns (e.g., Southwestern Scotian Shelf and Eastern Scotian Shelf (recent period), and Flemish Cap and Southern Grand Banks). Further exploration of the patterns in the residuals are provided in the Supplementary Material¹.

State-space model results

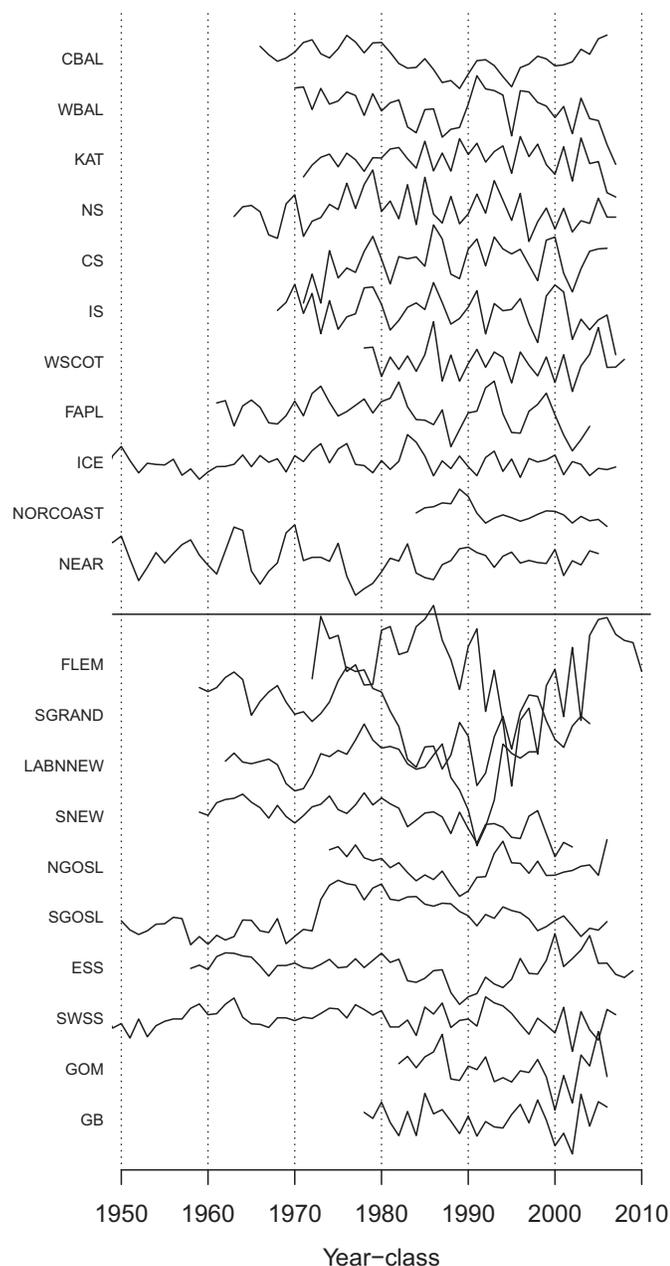
Model selection and diagnostics

Of the four noncovarying models investigated per region, the model with time-varying maximum reproductive rate alone fit best (Table 3). Adding in time-varying density dependence in addition to time-varying maximum reproductive rate resulted in a higher likelihood for the Northeast Atlantic fit, but not enough to offset the effect of the increased number of parameters on the AIC values. As such, there is little evidence to support time-varying density dependence for these populations (Table 3). We thus chose to only investigate the covariance implementation of the time-varying maximum reproductive rate model.

Violation of the assumption of normality of the innovations occurred in 10 of 21 stocks (Supplementary Figs. S3 and S4¹). The violations were typically caused by a small number of outlying

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0161>.

Fig. 1. Cod log survival residuals after removing the effects of adult abundance. Lines represent the residuals from fitting a time-invariant Ricker model to log survival. Each population is separated by two units on a natural logarithmic scale for display. The horizontal line divides Northeast Atlantic (top) and Northwest Atlantic (bottom) populations. Table 2 provides details of each population.



points, termed innovation outliers (Harvey 1991). We discuss the implications of the violations of normality below.

The assumption of independence of the innovations for a given stock was largely upheld, although the Southwestern Scotian Shelf and Irish Sea regions displayed mild but significant negative autocorrelation at lag 1 (Supplementary Figs. S5 and S6¹).

Trends in productivity

Many stocks display lower productivity today, compared with historical means. In the Northwest Atlantic (Fig. 2), the southern populations of Georges Bank, the Gulf of Maine, and the South-

Table 3. Summary of model fits.

Model name	-log likelihood	k	q	AIC
Northwest Atlantic				
Time-invariant	465.10	10	0	950.20
Time-varying productivity	199.16	20	10	458.32
Time-varying density dependence	335.91	20	10	731.82
Time-varying productivity and density dependence	199.16	30	20	498.32
Time-covarying productivity	109.88	65	20	389.76
Northeast Atlantic				
Time-invariant	338.52	11	0	699.04
Time-varying productivity	198.82	22	11	463.64
Time-varying density dependence	241.78	22	11	549.56
Time-varying productivity and density dependence	191.75	33	22	493.5
Time-covarying productivity	75.65	77	22	349.3

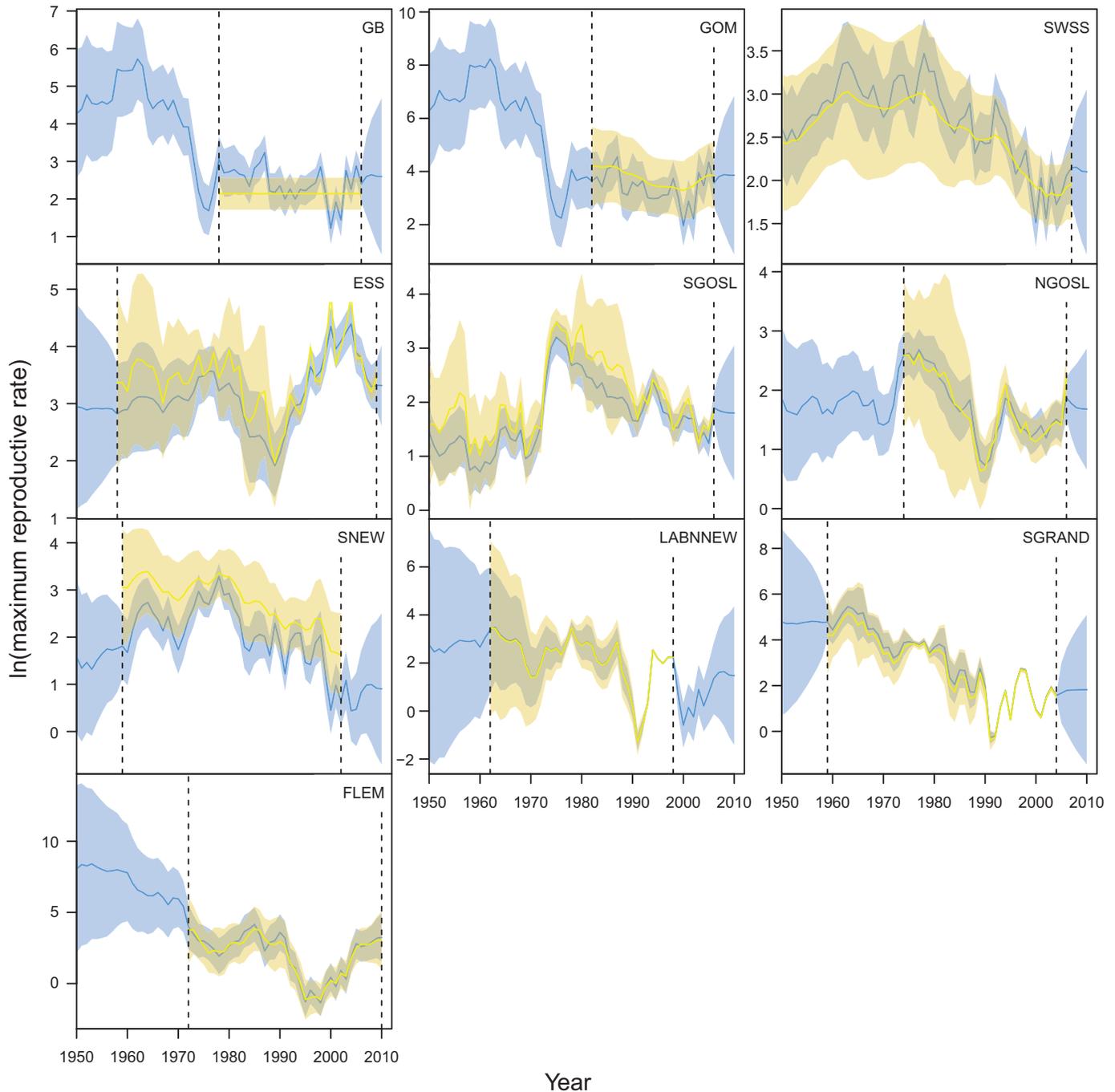
Note: k and q refer to the number of variance parameters and number of initialized states, respectively. AIC, Akaike's information criterion. Model descriptions are provided in Table 1.

western Scotian Shelf are currently close to a historic minimum (based on hindcasts for Georges Bank and the Gulf of Maine). While these hindcasts quickly become uncertain, this suggests that for those stocks the maximum reproductive rate has declined considerably.

The Eastern Scotian Shelf and Southern and Northern Gulf of St. Lawrence populations have potentially higher contemporary productivity than that observed or predicted at the earliest time points. All three stocks displayed markedly elevated productivity in the late 1970s and early 1980s. The Southern Newfoundland stock displayed increasing productivity until the 1980s and has been declining since. The Labrador – Northern Newfoundland population (Northern cod) displayed constant productivity to the late 1980s, where it dipped precipitously prior to the cod fishing moratorium in 1992. A similar but more consistently decreasing trend was observed for the Southern Grand Banks population, again with a precipitous decline in the early 1990s. Both stocks are currently at depressed productivity levels, although forecasts suggest slow though uncertain productivity increases in both. The Flemish Cap population displays differing productivity trends to those elsewhere in the Northwest Atlantic; while other populations reached a peak in productivity in the early 1980s, the Flemish Cap displayed a trough, similar to that observed in the mid- to late 1990s.

The longest series available in the Northeast Atlantic came from the Northeast Arctic and Icelandic populations. The Northeast Arctic population displayed very similar trends in the univariate and multivariate models (Fig. 3). The productivity of this stock fluctuates erratically but does not display any long-term directional trends from 1950 to 2010. Note that an earlier increase in productivity was observed for this population over the time period 1910–1950, it but is not plotted in Fig. 3 owing to the time span covered by most series being considerably shorter. The Norwegian Coastal stock has displayed a marked increase in productivity through the 1990s, after which it declined to a lower level. Similar to the Northeast Arctic population, the Icelandic population also displays marked process variability. Overall, this population reached a peak in the early 1980s and has been decreasing slowly and erratically but to levels higher than those in the 1950s. The Faroe Plateau population similarly reached a peak in the late 1970s and early 1980s, with a subsequent decline but to a lower level than that estimated in 1960. Further south, the West of Scotland population displayed constant productivity in the univariate fit, but more process variability in the multivariate fit. The productivity level for this population has remained approximately constant. The Irish Sea population displayed relatively constant

Fig. 2. Estimated maximum reproductive rates and 95% confidence intervals from univariate (yellow) and multivariate (blue) fits to the Northwest Atlantic cod populations. Dashed vertical lines represent the earliest and latest data points for that population. Predashed line fits are hindcasts from the multivariate Kalman smoother. Postdashed lines are smoothed forecasts.



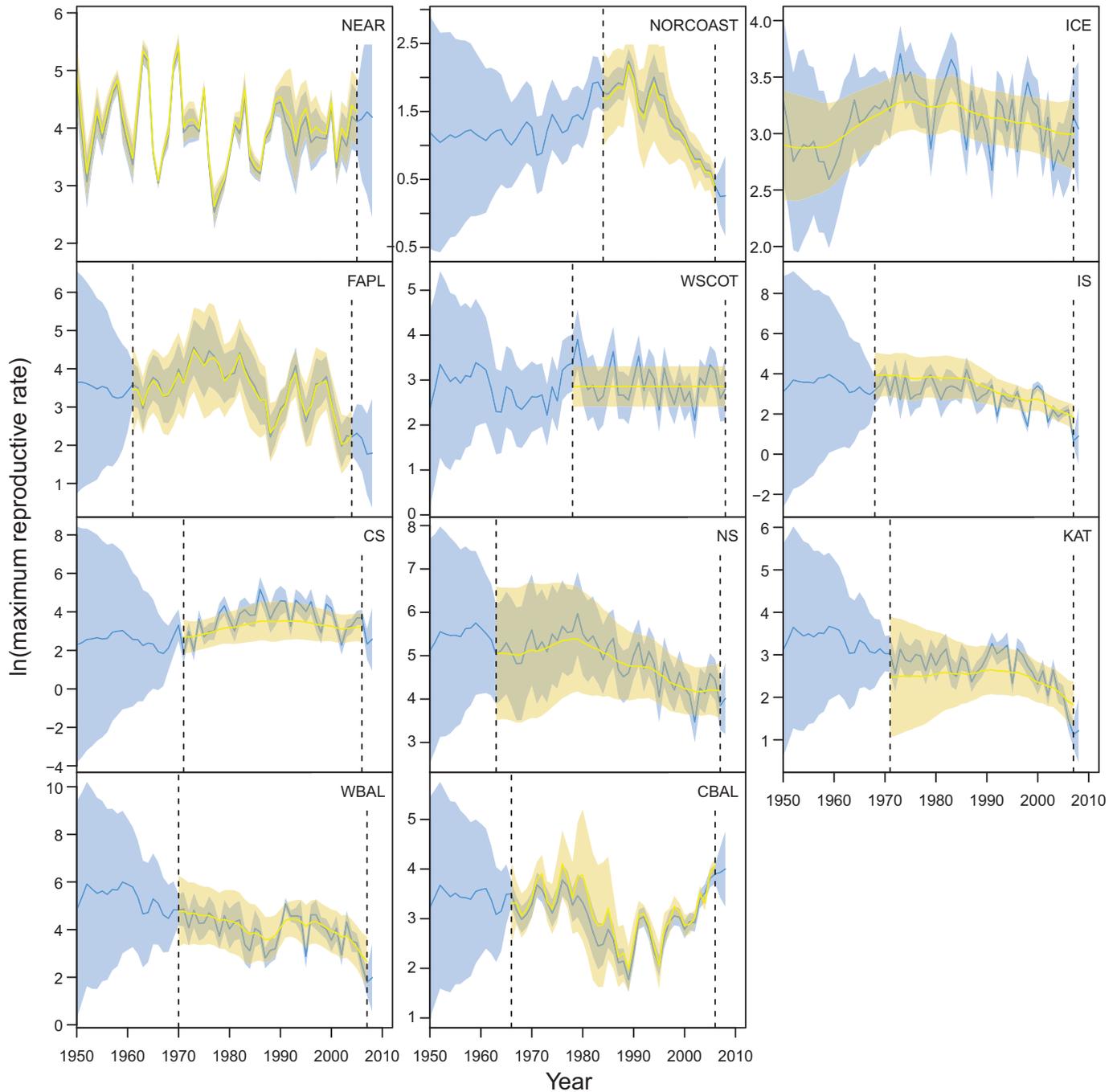
productivity until the late 1980s, and thereafter dropped to its presently low levels. The Celtic Sea population increased until the 1990s and has been slowly decreasing since, but to levels similar to those observed at the start of the series. The North Sea population displayed a highly uncertain increase until 1980 and a continuous decline to lower levels since. In the Kattegat, productivity appeared constant to the mid-1990s and has subsequently declined to low levels. The Western Baltic population declined until the late 1980s, then displayed a short uncertain period of increasing productivity and a subsequent decline to its presently low levels. In contrast, the central Baltic population also displayed an erratic

decline until the late 1980s, but thereafter has been increasing to higher productivity levels comparable to the highest observed in the series (Fig. 3).

Patterns in productivity across regions

The correlation of time-varying maximum reproductive rates across populations (ρ_a in eq. 9) shows marked patterns in the Northeast and Northwest Atlantic (Fig. 4). Some strong correlations exist in the Northwest Atlantic (e.g., the Georges Bank, Gulf of Maine, and Southwestern Scotian Shelf populations). Further north, the Labrador – Northern Newfoundland, Southern

Fig. 3. Estimated maximum reproductive rates and 95% confidence intervals from univariate (yellow) and multivariate (blue) fits to the Northeast Atlantic cod populations. Dashed vertical lines represent the earliest and latest data points for that population. Predashed line fits are hindcasts from the multivariate Kalman smoother. Postdashed lines are smoothed forecasts.

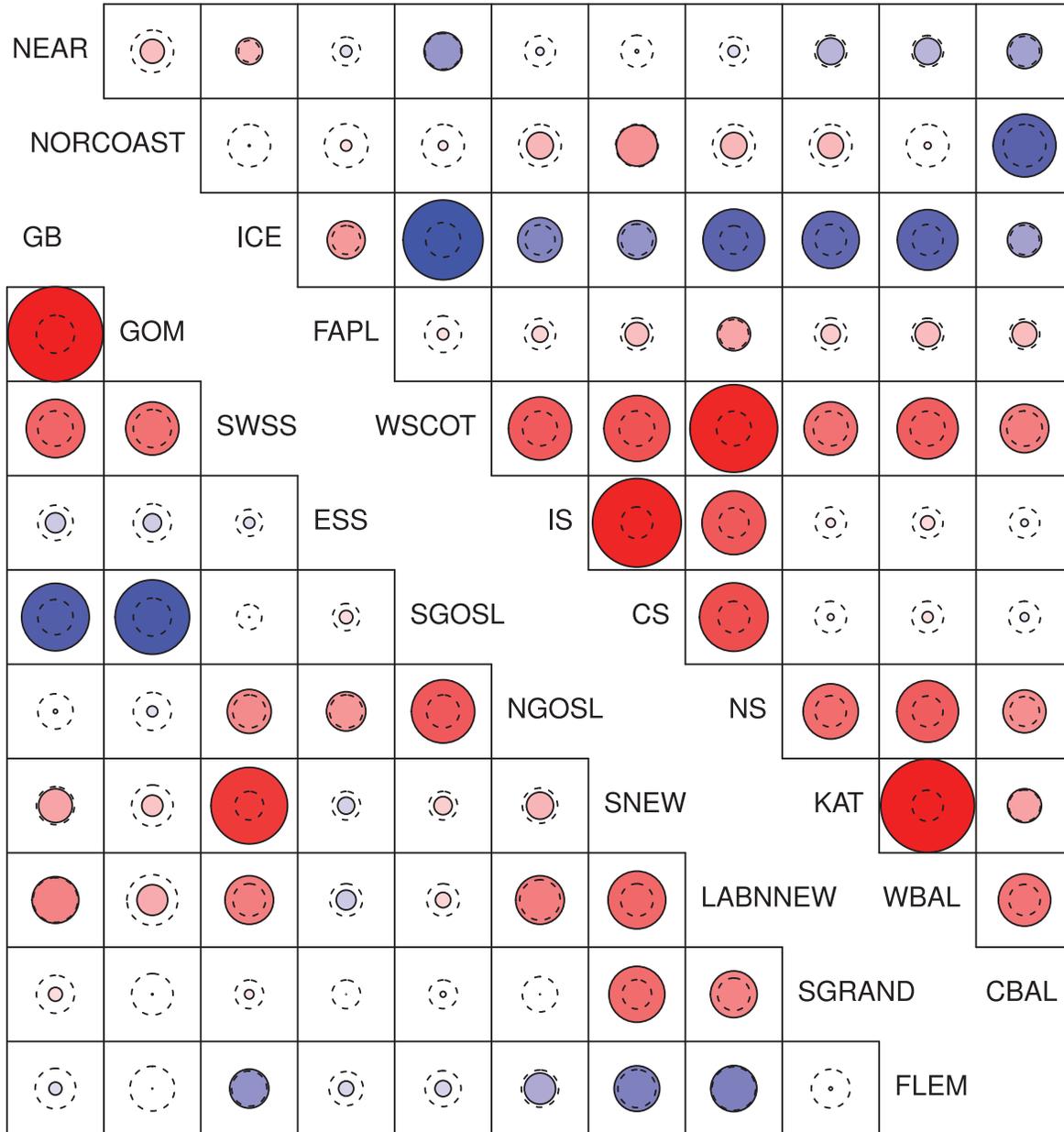


Newfoundland, and Southern Grand Banks populations display positive correlations. The Southwestern Scotian Shelf also displays positive correlations with distant stocks such as the Northern Gulf of St. Lawrence, Southern Newfoundland, and Labrador – Northern Newfoundland. Equally noticeable, however, is the isolation of several individual stocks from adjacent ones. For example, the Eastern Scotian Shelf stock displays no or weakly negative correlations with the nearby stocks of the Gulf of Maine and Georges Bank. Similarly, the Southern Gulf of St. Lawrence population displays no or negative correlation with all but the adjacent Northern Gulf population (Fig. 4). Outside the positive correla-

tions already highlighted, the Southern Grand Banks displays weak correlations with all other populations. Interestingly, the Flemish Cap displays weakly negative correlations with all populations (Fig. 4).

Northern populations of the Northeast Atlantic typically display no or negative correlations with more southerly populations (Fig. 4). Among the northerly Northeast Atlantic populations, the correlations are also weak. Most remarkably, the Icelandic population displays negative correlations with all populations outside the northern stocks other than the Faroe Plateau. The Faroe Plateau population displays weak correlations with all populations

Fig. 4. Correlations as estimated in the multivariate model for the Northwest Atlantic (lower triangle) and Northeast Atlantic (upper triangle). The strength of the correlation is represented by the radius of the circle, and the direction by the color (blue representing negative correlations and red positive). Radii greater than that of the dashed circles are approximately significant as calculated by $1.96\sqrt{1/N_{\text{overlap}}}$, where N_{overlap} is the number of pairwise overlapping points. Full region names are provided in Table 2.



apart from the Icelandic population. Two clusters of populations are apparent in the northeast Atlantic: the West of Scotland, Irish Sea, Celtic Sea, and North Sea; and the North Sea, Kattegat, Western Baltic, and Central Baltic populations, although the Central Baltic correlations are weaker (Fig. 4). The West of Scotland population displayed positive correlations with most southern populations.

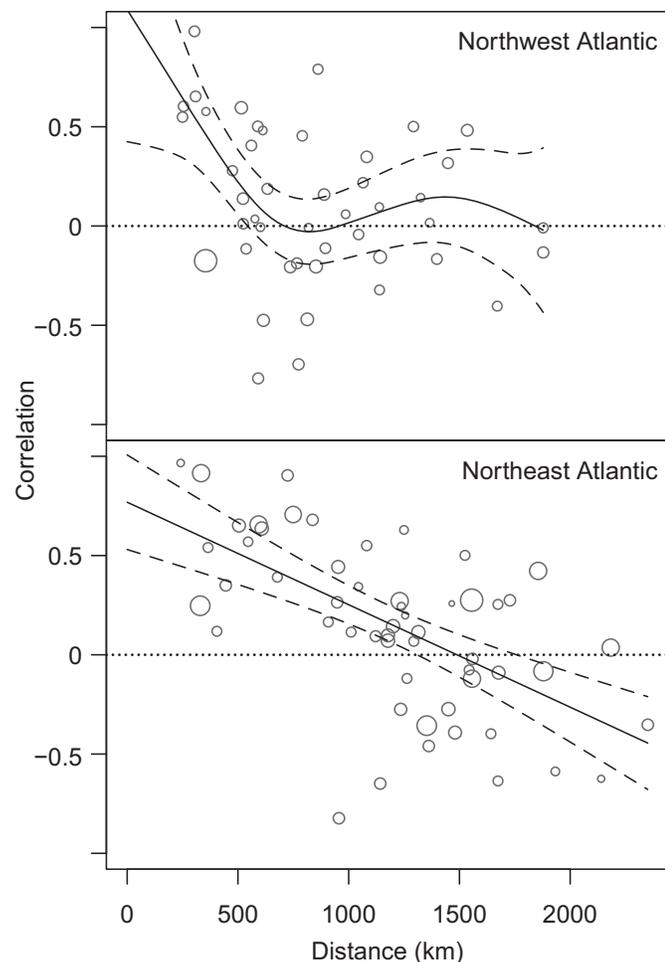
The correlation of the maximum reproductive rate between stock pairs decays with distance on both sides of the Atlantic (Fig. 5). Preliminary additive model fits indicate that the strength of the correlation appears to decay more quickly over geographic distance in the Northwest Atlantic (distance to a mean correlation of $0.5 \approx 330$ km) than the Northeast Atlantic (distance to a mean correlation of $0.5 \approx 520$ km) (Fig. 5).

Univariate–multivariate comparison

A comparison of the smoothed states from the univariate and multivariate formulations show similar trends for most populations, with overlapping confidence intervals from both methods (Figs. 2 and 3). The confidence intervals are tighter for the multivariate implementation, allowing for better inference on the dynamics. Some populations, such as Georges Bank, show dynamics not present in the univariate results (Fig. 2). Similar to the West of Scotland (Fig. 3), the univariate fit was flat, indicating no process variation in productivity when viewed in isolation. Yet, when analysed in a multivariate setting, distinct dynamics are present; indeed these were found to be strongly correlated with adjacent populations in both cases. The multivariate state estimates were

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by DALHOUSIE UNIVER on 03/04/14 For personal use only.

Fig. 5. The relationship between the estimated pairwise correlation of the time-varying productivity between regions and the geographic distance between the centroids of the populations. The radius of each point is proportional to the number of pairwise overlapping observations used to estimate the correlation. An additive model fit (solid line) and 95% confidence intervals (dashed lines) indicate overall trends with distance by region.



typically more variable than those of the univariate states (Figs. 2 and 3). Covarying productivity changes, which, in the univariate case, are attributed to measurement error, appear to be picked up as part of the process in the multivariate case.

Hindcasts prior to the start of the assessment quickly become uncertain as demonstrated by the rapidly expanding confidence intervals into the past where no data exist for that population (Figs. 2 and 3). Yet remarkably, some populations such as the Norwegian Coastal, West of Scotland, Georges Bank, and Gulf of Maine have relatively narrow confidence bands and dynamically changing hindcasts (Figs. 2 and 3). High productivity hindcasts for Georges Bank and the Gulf of Maine are largely driven by the strong negative correlation with the Southern Gulf of St. Lawrence in the period of overlap (Fig. 4), a region that had low productivity before 1970 (Fig. 2).

Fitted survival

The multivariate estimated log survival series differ qualitatively by population in the amount of measurement error estimated for that region (Fig. 6). For some populations (e.g., Northeast Arctic, Norwegian Coastal, Irish Sea, Western Baltic, Labrador – Northern Newfoundland, and Southern Grand Banks), the estimated measurement error is very small, resulting in nar-

row or negligible confidence intervals (Fig. 6). For other populations (e.g., Iceland, Faroe Plateau, West of Scotland, North Sea, Georges Bank, Southwestern Scotian Shelf, Flemish Cap), greater amounts of measurement error are estimated. Overall, the predicted series correspond well to the assessment data (Fig. 6).

Discussion

In developing a novel multivariate state-space model, we have shown that the maximum reproductive rate, an essential parameter that governs early life stage productivity, varies markedly through time. Our analysis for Atlantic cod populations indicated that the maximum reproductive rate for many of these was recently trending downwards, indicating some fundamental changes in stock biology, or, alternatively, in their environment. Importantly, these changes are independent of changes in adult abundance or the effects of density dependence. Regionally, there were clear productivity regimes across neighboring populations; these spatial trends appeared to be more strongly conserved in the Northeast Atlantic compared with Northwest Atlantic cod stocks.

Methodological advances and shortcomings

Advances

Our work is a logical extension of previous analyses by Myers et al. (1995b) on correlations in the recruitment dynamics among cod populations. Unlike that paper, and other analyses based on residuals about the stock–recruitment curve, our model considered all datasets at once and derived a correlation structure founded in population dynamics. Our correlations thus lend themselves to theories of fishing as opposed to interesting but ultimately limited-in-application correlations among residuals.

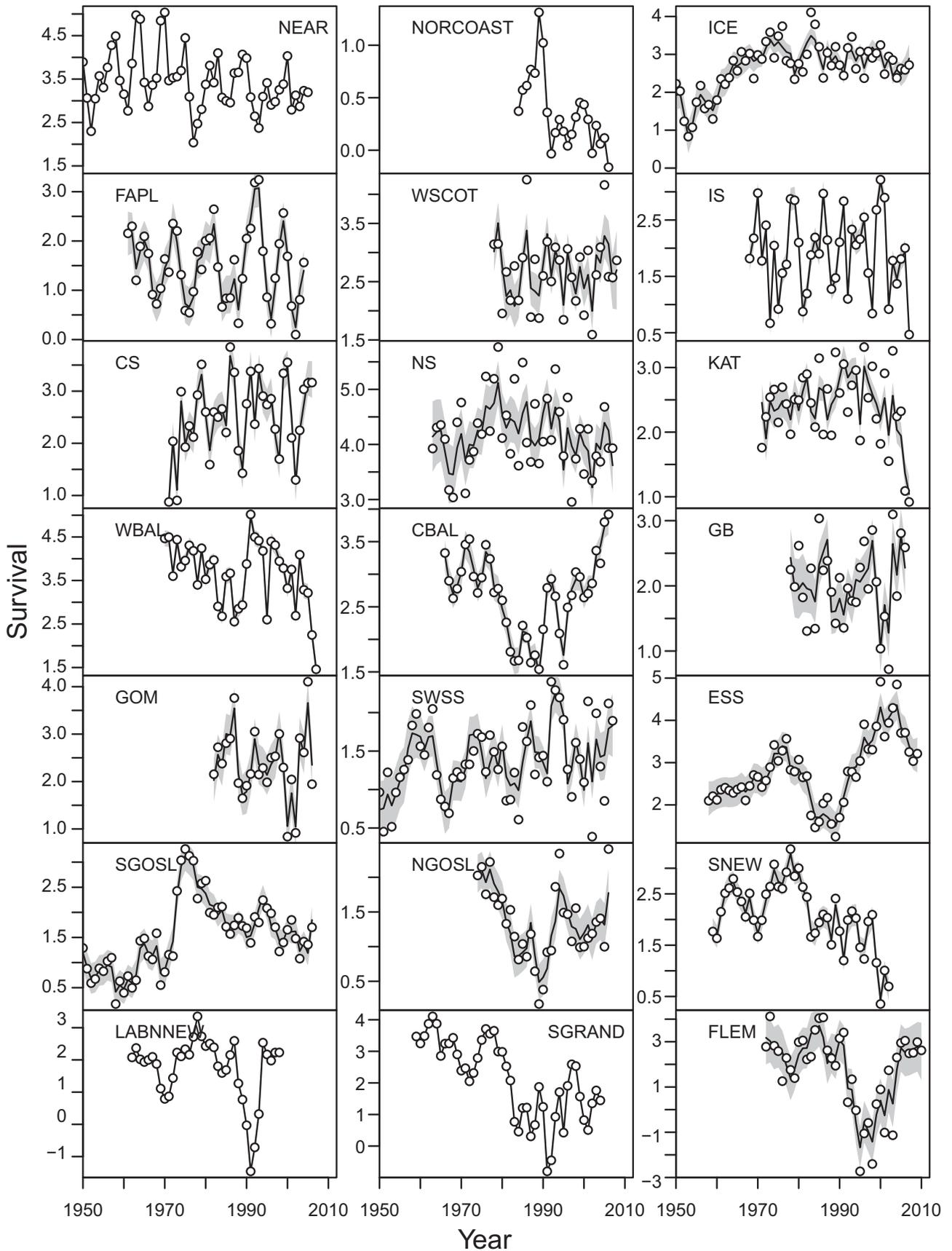
Time-varying density dependence was investigated in addition to the maximum reproductive rate and shown, via goodness-of-fit, to be relatively stable through time. Whether this reflects an inherent rigidity in the linear form of the model or a general feature on the ecology of the species remains to be investigated. We note, however, that state-space models are uniquely suited to the separation of what otherwise appear to be confounded processes.

Shortcomings

The spawner and recruit series we have used are not raw data but the output from complex population dynamics models that integrate catch and survey data to provide estimates of fishing mortality and abundance. Assumptions implicit in the assessment data and model may, therefore, affect our results. To our knowledge, none of the assessments we used have fixed parameters regarding recruitment. Misreporting of the catch as well as nonconstant adult natural mortality may also affect the estimated spawner and recruit series. Of particular concern to our inference is discarding of prerecruit fish, particularly where this has trended in time. While these issues are of concern, we treated the stock assessment as the maximal state of knowledge on the stock and based our inferences thereon, noting that our state-space model includes both process and measurement error variance, which may alleviate some of these issues.

We assumed normality throughout, which allowed us to implement a relatively straightforward multivariate model using the Kalman filter and smoother. Yet violations of the assumption of normality occurred quite frequently (see Supplementary Material¹). It is difficult to distinguish between structural breaks in the process and outlying events; both will appear as innovation outliers when investigated. Either way, the effect is to inflate the process error variance (Harvey 1991). Assuming longer tailed distributions for the disturbances, using methods such as those presented in Kitagawa (1987) are likely to yield better fits, but multivariate implementations of these models were considered beyond the scope of the present manuscript. We note that such

Fig. 6. Observed (points) and fitted (solid line) log survival by population. Grey shading represents the 95% confidence intervals. Corresponding area names are provided in Table 2.



Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by DALHOUSIE UNIVER on 03/04/14
For personal use only.

non-normal methods may be particularly useful when identifying structural breaks in productivity (Vert-pré et al. 2013), potentially yielding a very general class of recruitment models.

Myers et al. (1999) demonstrated the suitability of the Ricker model in estimating the maximum reproductive rate. The Ricker model was particularly convenient in this application owing to its linearization, allowing use of the Kalman filter and smoother techniques. The Beverton–Holt stock–recruitment function can also be linearized on the inverse scale (see Nelder (1966) for a discussion of the Michaelis–Menten equation as a first-order inverse polynomial) but would likely require a non-normal error assumption. Nonlinear, non-normal functions would require approximate or sampling-based solutions to parameter and state estimation. We note, however, that the Beverton–Holt has an equivalent parameter governing the intrinsic productivity (the slope at the origin of the stock–recruit function) and only differs in the form of density dependence. Our observed trends in productivity should therefore be relatively robust to the particular stock–recruitment functional form.

Estimating the slope at the origin requires extrapolation, which has proved very difficult for the related question of estimating steepness in many assessment methods. Allowing this parameter to vary in time adds an additional level of complication. Yet the confidence intervals surrounding the dynamic maximum productivity states we have estimated allow for inference on changes. Many of the populations observed here have at one time been reduced to very low spawner biomasses, sometimes over protracted periods (e.g., Northern cod). Atlantic cod may therefore be a suitable model species to test these methods. Moreover, we note that state-space time-series models are extremely powerful methods for detecting signals from data.

Finally, we note that although the unstructured covariance matrix makes the fewest a priori assumptions on the correlations among stocks, the number of parameters increases proportionally to the square of the number of stocks. There exist many formulations for the structure of the covariance matrix \mathbf{Q}_a , such as exchangeable (same correlation between all populations), exponential, and half-Gaussian, among others (Diggle et al. 2003). The correlation may also be made an internal function of a distance measure (likely geographic distance, but also other distances, for example, genetic, might be of interest) between the populations. Such flexibility opens many additional avenues for further research on productivity dynamics and interrelationships among stocks.

Productivity dynamics

Observed long-term trends in the maximum reproductive rate indicate that populations may go through longer periods of both high and low productivity. For example, the Eastern Scotian Shelf population exhibited relatively stable maximum reproductive rate until the late 1980s, decreasing through the 1990s and then rapidly increasing to a higher level, with a recent decrease (Fig. 2). The Gulf of St. Lawrence populations have also exhibited similar changes. Qualitatively, some populations exhibit marked increases and decreases in productivity (Eastern Scotian Shelf, Southwestern Scotian Shelf), whereas others appear to have entered a different productivity regime (Georges Bank, Gulf of Maine), albeit as inferred from hindcasts of relatively short time series (Fig. 2). For the Gulf of Maine stock, the hindcasted result conflicts somewhat with the long historical assessment for this stock (Butterworth and Rademeyer 2008). The historical assessment showed low recruitment at high spawning stock biomass before 1970, and once the recruitment model was accounted for, variable residuals did not show marked increases in productivity before 1970, although the Ricker residuals from 1965 to 1955 were consistently positive. The large increases in hindcasted productivity result from a strong negative correlation with the Southern Gulf of St. Lawrence stock in the period of overlap. It is possible that for these stocks the

covariance matrix (Fig. 4) is nonstationary (Kelly et al. 2009), a hypothesis that could be further investigated in a state-space framework with dynamic covariance structures (Petris et al. 2009).

The Newfoundland populations (Southern Newfoundland, Labrador – Northern Newfoundland, Southern Grand Banks, and Flemish Cap) are the only stocks to have estimated time-varying maximum reproductive rates close to or even below the point of replenishment of the population at zero fishing mortality (Fig. 2, zero line). While the Flemish Cap population productivity recovered from a low in the mid- to late 1990s, the recovery of the reproductive rates in the other Newfoundland stocks has been considerably slower, as inferred from the smoothed multivariate forecasts.

Overall, the Northeast Atlantic stocks displayed less dramatic changes in productivity, although the Norwegian Coastal, Faroe Plateau, and Central Baltic populations exhibited marked changes. Many of the Northeast Atlantic populations have exhibited a recent decline in productivity; most noticeable relative to the earliest hindcasts are the Irish Sea, North Sea, Kattegat, and Western Baltic (Fig. 3).

Covariance of the trends

When viewed together, the consistent patterns in maximum reproductive rate observed across some populations (Fig. 4) might be indicative of spatially defined productivity regimes or “provinces”, perhaps determined by prevailing environmental conditions or differences in stock structure. Yet the picture is not as unequivocal as previously thought. Based upon the coherence of spawning stock biomass or recruitment series in the Northwest Atlantic, Rothschild (2007) concluded that strong coherence is likely the result of common environmental conditions. However, coherence of the spawning stock biomass may also reflect factors other than the environment (e.g., coherent fishing mortality patterns). We have focused on recruitment, specifically trends in the maximum reproductive rate, which is a combination of fecundity and density-independent (environmental forcing) mortality (Ricker 1958). Allowing the maximum reproductive rate to vary allows changes in the productivity of the population unrelated to spawner abundance or the strength of density dependence to be investigated. Environmental effects can therefore be isolated from the effects of density and adult abundance (see comments on maternal effects below). While considerable correlation appears between some populations of the Northwest Atlantic with some clustering evident (Fig. 4), the coherence at this life stage is not consistent across larger regions (Fig. 4). In fact, some populations within the Northwest Atlantic exhibit negative correlations, even those in relative proximity (Fig. 4). The estimated pairwise correlation also drops off considerably quicker over geographical distance in the Northwest Atlantic (Fig. 5) than previously inferred via correlations in recruitment residuals (Myers et al. 1995b, 1997). This indicates that the processes governing productivity during the early life history stages in this region may operate at a more local scale than previously thought.

In the Northeast Atlantic, the northern populations of Icelandic and Northeast Arctic cod exhibit weakly positive correlation of their time-varying maximum reproductive rates, but vary inversely with populations of more southern latitudes (Fig. 4). These results suggest these populations respond in an opposite direction to those of southern latitudes. The Icelandic population is noteworthy in that it displays negative correlation with all southern populations. Myers et al. (1995b) also noticed this from the correlation amongst the residuals in recruitment, but those correlations were weak using the series available at the time. The correlations in the raw and detrended residuals are also weak using the most recent series (Supplementary Materials¹) and point towards the utility of the time-varying parameter approach implemented here.

Adopting a multivariate approach allows for information to be shared across populations, in terms of the covariances among populations. In many regions, similar overall trends are observed in the univariate and multivariate implementations (Figs. 2 and 3). The multivariate implementation, however, enables the strength of the correlation between populations to be estimated within the model, thus accounting for multiple sources of uncertainty. The process variability of the estimated states increases in the multivariate setting, with some regions that exhibited constant reproductive rate in the univariate setting showing greatly increased dynamics in the multivariate setting (Figs. 2 and 3). Two regions, Georges Bank and West of Scotland, emphasize this observation. The Georges Bank multivariate implementation exhibits very different dynamics compared with those of the univariate case. Strong correlations were estimated between the Georges Bank, Gulf of Maine, and Southwestern Scotian Shelf populations (Fig. 4). This correlation influences the states for the Georges Bank population. As there were no constraints on the correlation parameters (unstructured), the multivariate implementation may be more reflective of the actual dynamics, inasmuch as information is shared across populations. The West of Scotland also displayed strong correlations with adjacent populations (Fig. 4), but the multivariate implementation largely follows that of the univariate, though with more process variability.

Hypotheses for observed changes

While allowing the maximum reproductive rate to vary as a stochastic process, the approach taken here is without explicit mechanism. Here we discuss potential hypotheses for the observed changes, bearing in mind that the maximum reproductive rate is a combination of density-independent mortality and fecundity.

Density-independent effects

Mantzouni et al. (2010) presented a hierarchical model linking the maximum reproductive rate to changes in temperature for Atlantic cod. Similarly, Brander and Mohn (2004) presented evidence for the effects of broad-scale climatic indices on recruitment success. Planque and Frédou (1999) showed relationships between temperature and raw recruitment. Drinkwater (2005) used some of these relationships to predict future scenarios, with range expansions in the northern areas and range contractions and loss of populations in southern areas. Overall, the trends we estimated present a mosaic of responses that are considerably more dynamic than a straightforward temperature effect could impart. For example, the Georges Bank and Gulf of Maine populations responded as predicted, whereas the Celtic Sea population, inhabiting the warmest region of all, exhibited increases in productivity until the late 1990s and a decline to levels comparable to those observed at the earliest time point for this population, higher than the uncertain hindcast. Similarly, the Newfoundland stocks are predicted to increase in size (Drinkwater 2005), although the productivity of these populations has declined to very low levels. A solely unidirectional response was not inferred by Drinkwater (2005), nor was there a distinction between carrying capacity and productivity, but it is clear from our results that there are other drivers operating to affect productivity in addition to temperature effects. The finding of the marked decrease in pairwise correlation with distance in the Northwest Atlantic would further suggest that the effects are more localized than previously thought in that region.

Beaugrand et al. (2003) suggested that an interaction between temperature changes and zooplankton dynamics could adversely affect the reproductive success of cod via the match-mismatch hypothesis (Cushing 1975, 1996). Boyce et al. (2010) reported broad-scale changes in chlorophyll concentrations with marked declines in many regions, including the North Atlantic, though local increases were observed for the North Sea and Baltic. Changes in

plankton dynamics may reduce the condition of early life history stage larvae and increase density-independent mortality (Cushing 1975). Such changes could be reflected in the observed changes to the maximum reproductive rate. Recently, Kristiansen et al. (2011) found that the importance of match-mismatch dynamics increased with latitude, adding additional complexity to the predicted response.

Many small pelagic species such as Atlantic herring and Atlantic mackerel have increased in abundance since the early 1980s (Worm et al. 2009). Some of these species are observed to prey on the early life history stages of groundfish, including cod (Daan et al. 1985; Köster and Möllmann 2000; Segers et al. 2007). Swain and Sinclair (2000) showed a lower recruitment success of cod in the Southern Gulf of St. Lawrence with increased herring and mackerel abundance. It is debated whether this occurs in the adjacent Eastern Scotian Shelf region (Frank et al. 2011; Swain and Mohn 2012). Fauchald (2010) investigated the effect of zooplankton, temperature, and small pelagic species abundance on cod recruitment and concluded that predation by small pelagics was an important source of prerecruit mortality. In a hierarchical investigation of the effect on recruitment, Minto and Worm (2012) found an overall negative effect of herring abundance on young cod survival but with considerable regional variation.

Maternal effects

Trippel et al. (1997) showed that using older fish as a measure of spawning potential provided a better relationship with recruitment. As such, changes in the age composition of the population can affect the reproductive output (Hutchings and Myers 1993; Wright and Gibb 2005). Marshall et al. (2006) also showed changes in egg production of cod in the Northeast Arctic via changes in spawner composition. In a meta-analysis of the effect of the diversity of spawner ages on recruitment and recruitment variability, Brunel (2010) observed that such maternal effects, particularly age diversity, can be important for some species, including cod, but that the effects are not taxonomically universal. It is also possible that the effects manifest through potentially complex interactions between maternal effects and environmental conditions (Green 2008).

The degree to which the observed changes are common across, or specific to, certain populations and regions should assist in the reduction of plausible hypotheses. Candidate hypotheses must be capable of explaining the scale of the observed changes recorded here (Figs. 4 and 5) (Myers et al. 1995b). Estimated trends in prerecruit productivity that are independent of adult density and density-dependent effects, such as those proposed here, would also feature in such a testing framework. The current approach may also be amenable to alternative tests of time-series forcing such as Granger causality (Hamilton 1994).

Disentangling density-independent and maternal effects

The penultimate step in the derivation of the Ricker stock-recruitment model combines the product of fecundity and density-independent mortality into one term — the slope at the origin — which, when appropriately scaled, is the maximum reproductive rate (Myers et al. 1996). Where information is available on the temporal dynamics of fecundity, these may be included directly in the recruitment function, providing for a cleaner interpretation of changes attributable to density-independent effects. Ricker (1973) makes explicit reference to this approach. Unfortunately, the paucity of long-term monitoring of fecundity (Trippel et al. 1997) may preclude such an investigation, although some populations, such as the Northeast Arctic cod, could be amenable to such investigations.

Population viability

Rescaling the slope at the origin using the weight of spawners per recruit at zero fishing mortality ($SPR_{F=0}$) allows the long-term

viability of the population to be investigated. A maximum reproductive rate of one corresponds to equilibrium replacement, whereas values below one would indicate population decline with potential extinction risk. Many of the populations have values much greater than one (exponent of the natural logarithm of the maximum reproductive series in Figs. 2 and 3), as noted by Myers et al. (1996), although some populations such as the Northern Gulf of St. Lawrence (around 1990), Eastern Scotian Shelf (recently), and Western Baltic (around 1990) had values very close to one. The Newfoundland populations had maximum reproductive rates lower than one for short periods of time. Were they sustained, these values would result in progressive decline, even without fishing mortality, and therefore heightened extinction risk (Myers and Mertz 1998). It is important to note that the calculation of $SPR_{F=0}$ involves natural mortality of the adult population. In many cod populations this is fixed at 0.2, whereas Swain and Chouinard (2008) and Trzcinski et al. (2006) have documented marked increases in adult natural mortality that would imply a lower $SPR_{F=0}$ value than those used here. This would affect where the replacement line occurs for the interpretation of extinction risk, but not the trends nor correlations we estimated. Other populations such as the Norwegian Coastal population, Irish Sea, Kattegat, and the Western Baltic display worrying contemporary trends of decreasing productivity (Fig. 3).

Management implications

Short-term forecasts are used in most stock assessments to project the population trajectory under a range of exploitation scenarios (Quinn and Deriso 1999). The geometric mean of the recruitment rate averaged over a number of recent years is typically used for this. Such an approach may, therefore, reflect present productivity conditions, unless marked trending patterns are present in recent recruitment. Where our approach significantly departs from traditional fisheries management methods is in the recognition that the maximum reproductive rate is not static and can in fact change quite markedly from year to year. The consequence of this observation is that biological reference points established thereon also have to be dynamic. The commonly used approach of estimating a single reference point effectively produces management advice that is geared to average past conditions. Yet, the present productivity may have departed considerably, putting the population at risk of overfishing (or underfishing) given changed productivity levels.

Ecosystem approaches to fisheries management holistically approach the question of dynamic productivity in a dynamic environment, but the large number of potential interactions (largely focused on adults) as well as associated uncertainties have delayed applications to single-species management advice. Ultimately, a mechanistic understanding of the broader system is required, but at the single-species level the time-varying approach we developed may provide a method for integrating empirically across the plethora of environmental and biological drivers. As such, we may refer to time-varying population dynamics models as an "implicit ecosystem approach".

In conclusion, marked temporal and spatial variation was observed in a key population parameter, the maximum reproductive rate, within and across populations for Atlantic cod. Our method develops on previous analyses of correlations among recruitment residuals, primarily through its foundation in population dynamics theory. The method allows for simultaneous estimation of time-varying recruitment dynamics across multiple populations. It demonstrates how these relationships change with geographic distance, identifying similar productivity regimes among neighbouring populations. The observed trends displayed some synchronicity across populations, but also finer scale variability not readily explained by panregional hypotheses. The explicit investigation of the management implications can be pro-

vided through traditional theory extended for time-varying components (Collie et al. 2012).

Acknowledgements

We thank Atlantic cod stock assessment scientists and working groups upon whose assessments our work is based. We are very grateful to Julia Baum, Corinne Barber, Wade Blanchard, Kenneth Frank, Jeffrey Hutchings, Olaf Jensen, Terrance Quinn II, and Daniel Ricard for helpful discussions and critiques. Two anonymous reviewers greatly improved the quality of the analyses and presentation. This work was supported by the Irish Department of Education, Technological Research Sector Program Strand III, the Sobey Fund for Oceans, and the Natural Sciences and Engineering Research Council of Canada (NSERC).

References

- Allen, K.R. 1963. Analysis of stock-recruitment relations in Antarctic fin whales. Rapp. Proc. Verb. Reun. Cons. Perm. Intl. Explor. Mer, **164**: 132–137.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., and Reid, P.C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, **426**(6967): 661–664. doi:10.1038/nature02164. PMID:14668864.
- Boyce, D.G., Lewis, M.R., and Worm, B. 2010. Global phytoplankton decline over the past century. Nature, **466**(7306): 591–596. doi:10.1038/nature09268. PMID:20671703.
- Brander, K., and Mohn, R. 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **61**(9): 1558–1564. doi:10.1139/f04-087.
- Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. ICES J. Mar. Sci. **67**(9): 1921–1930. doi:10.1093/icesjms/fsq032.
- Butterworth, D.S., and Rademeyer, R.A. 2008. Statistical catch-at-age analysis vs. ADAPT-VPA: the case of Gulf of Maine cod. ICES J. Mar. Sci. **65**: 1717–1732. doi:10.1093/icesjms/fsn178.
- Cairns, D.K. 2001. An evaluation of possible causes of the decline in pre-fishery abundance of North American Atlantic salmon. Can. Tech. Rep. Fish. Aquat. Sci. 2358.
- Cardinale, M., and Hjelm, J. 2006. Marine fish recruitment variability and climate indices. Mar. Ecol. Progr. Ser. **309**: 307–309.
- Clark, J.S. 2007. Models for ecological data: an introduction. Princeton University Press, Princeton, N.J., USA.
- Collie, J.S., Peterman, R.M., and Zuehlke, B.M. 2012. A fisheries risk-assessment framework to evaluate trade-offs among management options in the presence of time-varying productivity. Can. J. Fish. Aquat. Sci. **69**(2): 209–223. doi:10.1139/f2011-148.
- Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, London.
- Cushing, D.H. 1996. Towards a science of recruitment in fish populations. Excellence in ecology. Ecology Institute, Oldendorf/Luhe, Germany.
- Daan, N., Rijnsdorp, A.D., and van Overbeeke, G.R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Trans. Am. Fish. Soc. **114**: 499–506. doi:10.1577/1548-8659(1985)114<499:PBNSHC>2.0.CO;2.
- Diggie, P.J., Heagerty, P.J., Liang, K.Y., and Zeger, S.L. 2003. Analysis of longitudinal data. Oxford University Press, Oxford, UK.
- Dorner, B., Peterman, R.M., and Haeseker, S.L. 2008. Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter. Can. J. Fish. Aquat. Sci. **65**(9): 1842–1866. doi:10.1139/F08-094.
- Drinkwater, K.F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES J. Mar. Sci. **62**(7): 1327–1337. doi:10.1016/j.icesjms.2005.05.015.
- Durbin, J.J., and Koopman, S.J. 2001. Time series analysis by state space methods. Oxford University Press, Oxford, UK.
- Fauchald, P. 2010. Predator-prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology, **91**(8): 2191–2197. doi:10.1890/09-1500.1. PMID:20836439.
- Frank, K.T., Petrie, B., Fisher, J.A.D., and Leggett, W.C. 2011. Transient dynamics of an altered large marine ecosystem. Nature, **477**: 86–89. doi:10.1038/nature10285. PMID:21796120.
- Fryer, R., Needle, C., and Reeves, S. 1998. Kalman filter assessments of cod, haddock and whiting in Vía. Tech. Rep., ICES, Copenhagen, Denmark.
- Green, B.S. 2008. Maternal effects in fish populations. Adv. Mar. Biol. **54**: 1–105. doi:10.1016/S0065-2881(08)00001-1. PMID:18929063.
- Hamilton, J.D. 1994. Time series analysis. Princeton University Press, Princeton, N.J., USA.
- Harding, D., and Talbot, J.W. 1973. Recent studies on the eggs and larvae of the plaice (*Pleuronectes platessa* L.) in the Southern Bight. Rapp. Proc. Verb. Reun. Cons. Perm. Intl. Explor. Mer, **164**: 261–269.

- Harvey, A. 1991. Forecasting, structural time series models and the Kalman filter. Cambridge University Press, Cambridge, UK.
- Houde, E.D. 2008. Emerging from Hjort's shadow. *J. Northw. Atl. Fish. Sci.* **41**: 53–70. doi:10.2960/J.v41.m634.
- Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **50**(11): 2468–2474. doi:10.1139/f93-271.
- Ives, A.R., Dennis, B., Cottingham, K.L., and Carpenter, S.R. 2003. Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* **73**(2): 301–330. doi:10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2.
- Kelly, J.E., Frank, K.T., and Leggett, W.C. 2009. Degraded recruitment synchrony in Northwest Atlantic cod stocks. *Mar. Ecol. Prog. Ser.* **393**: 131–146. doi:10.3354/meps08241.
- Kitagawa, G. 1987. Non-Gaussian state-space modeling of nonstationary time series. *J. Am. Stat. Assoc.* **82**: 1032–1041. doi:10.2307/2289375.
- Köster, F., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J. Mar. Sci.* **57**(2): 310–323. doi:10.1006/jmsc.1999.0528.
- Kristiansen, T., Drinkwater, K.F., Lough, R.G., and Sundby, S. 2011. Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS ONE*, **6**(3): e17, 456.
- Lambert, Y. 2008. Why should we closely monitor fecundity in marine fish populations? *J. Northw. Atl. Fish. Sci.* **41**: 93–106. doi:10.2960/J.v41.m628.
- Mace, P.M., and Sissenwine, M.P. 1993. How much spawning per recruit is enough? In Risk evaluation and biological reference points for fisheries management. Edited by S.J. Smith, J.J. Hunt, and D. Rivard. *Can. Spec. Publ. Fish. Aquat. Sci.* **120**: 101–118.
- Mantzouni, I., and MacKenzie, B.R. 2010. Productivity responses of a widespread marine piscivore, *Gadus morhua*, to oceanic thermal extremes and trends. *Proc. R. Soc. B Biol. Sci.* **277**(1689): 1867–1874. doi:10.1098/rspb.2009.1906.
- Mantzouni, I., Sørensen, H., O'Hara, R.B., and MacKenzie, B.R. 2010. Hierarchical modelling of temperature and habitat size effects on population dynamics of North Atlantic cod. *ICES J. Mar. Sci.* **67**(5): 833–855. doi:10.1093/icesjms/ fsp291.
- Marshall, C.T., Needle, C.L., Thorsen, A., Kjesbu, O.S., and Yaragina, N.A. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock-recruit theory and management. *Can. J. Fish. Aquat. Sci.* **63**(5): 980–994. doi:10.1139/f05-270.
- Minto, C. 2011. Ecological inference from variable recruitment data. Ph.D. thesis, Dalhousie University, Halifax, N.S., Canada.
- Minto, C., and Worm, B. 2012. Interactions between small pelagic fish and young cod across the North Atlantic. *Ecology*, **93**(10): 2139–2154. doi:10.1890/10-2036.1. PMID:23185876.
- Myers, R.A. 1998. When do environment–recruitment correlations work? *Rev. Fish. Biol. Fish.* **8**(3): 285–305. doi:10.1023/A:1008828730759.
- Myers, R.A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES J. Mar. Sci.* **58**(5): 937–951. doi:10.1006/jmsc.2001.1109.
- Myers, R.A., and Mertz, G. 1998. The limits of exploitation: a precautionary approach. *Ecol. Appl.* **8**(Suppl. 1): S165–S169. doi:10.2307/2641375.
- Myers, R.A., Bridson, J., and Barrowman, N.J. 1995a. Summary of worldwide spawner and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci.* 2024.
- Myers, R.A., Mertz, G., and Barrowman, N.J. 1995b. Spatial scales of variability in cod recruitment in the North Atlantic. *Can. J. Fish. Aquat. Sci.* **52**(9): 1849–1862. doi:10.1139/f95-778.
- Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1996. Hypotheses for the decline of cod in the North Atlantic. *Mar. Ecol. Prog. Ser.* **138**(1): 293–308. doi:10.3354/meps138293.
- Myers, R.A., Mertz, G., and Bridson, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Can. J. Fish. Aquat. Sci.* **54**(6): 1400–1407. doi:10.1139/f97-045.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/f99-201.
- Nelder, J.A. 1966. Inverse polynomials, a useful group of multi-factor response functions. *Biometrics*, **22**: 128–141. doi:10.2307/2528220.
- Peterman, R.M., Pyper, B.J., and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**(7): 809–824. doi:10.1139/f03-069.
- Petris, G., Petrone, S., and Campagnoli, P. 2009. Dynamic linear models with R. Springer, New York.
- Planque, B., and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **56**(11): 2069–2077. doi:10.1139/f99-114.
- Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- R Development Core Team. 2012. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>. ISBN 3-900051-07-0.
- Ricard, D., Minto, C., Jensen, O.P., and Baum, J.K. 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish. Fish.* **13**: 380–398. doi:10.1111/j.1467-2979.2011.00435.x.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**(5): 559–623. doi:10.1139/f54-039.
- Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Board Can.* **119**: 1–300.
- Ricker, W.E. 1973. Critical statistics from two reproduction curves. *Rapp. Proc. Verb. Reun. Cons. Perm. Int. Explor. Mer.* **174**: 333–340.
- Rothschild, B.J. 2007. Coherence of Atlantic cod stock dynamics in the northwest Atlantic Ocean. *Trans. Am. Fish. Soc.* **136**(3): 858–874. doi:10.1577/T06-213.1.
- Segers, F.H.I.D., Dickey-Collas, M., and Rijnsdorp, A.D. 2007. Prey selection by North Sea herring (*Clupea harengus*), with special reference to fish eggs. *ICES J. Mar. Sci.* **64**: 60–68.
- Shelton, P.A., Sinclair, A.F., Chouinard, G.A., Mohn, R., and Duplisea, D.E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **63**(2): 235–238. doi:10.1139/f05-253.
- Swain, D.P., and Chouinard, G.A. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **65**(11): 2315–2319. doi:10.1139/F08-175.
- Swain, D.P., and Mohn, R.K. 2012. Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. *Can. J. Fish. Aquat. Sci.* **69**(6): 997–1001. doi:10.1139/f2012-045.
- Swain, D.P., and Sinclair, A.F. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **57**(7): 1321–1325. doi:10.1139/f00-104.
- Trippel, E., Kjesbu, O.S., and Solemial, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In *Early life history and recruitment in fish populations*. Chapman and Hall, New York. pp. 575–596.
- Trzcinski, M.K., Mohn, R., and Bowen, W.D. 2006. Continued decline of an Atlantic cod population: how important is gray seal predation? *Ecol. Appl.* **16**(6): 2276–2292. doi:10.1890/1051-0761(2006)016[2276:CDOAAC]2.0.CO;2. PMID:17205904.
- Vert-pre, K.A., Amoroso, R.O., Jensen, O.P., and Hilborn, R. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proc. Natl. Acad. Sci.* **110**(5): 1779–1784. doi:10.1073/pnas.1214879110. PMID:23322735.
- Worm, B., and Myers, R.A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, **84**(1): 162–173. doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D. 2009. Rebuilding global fisheries. *Science*, **325**(5940): 578–585. doi:10.1126/science.1173146. PMID:19644114.
- Wright, P.J., and Gibb, F.M. 2005. Selection for birth date in North Sea haddock and its relation to maternal age. *J. Anim. Ecol.* **74**(2): 303–312. doi:10.1111/j.1365-2656.2005.00924.x.
- Zeng, Z., Nowierski, R.M., Taper, M.L., Dennis, B., and Kemp, W.P. 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. *Ecology*, **79**(6): 2193–2209. doi:10.1890/0012-9658(1998)079[2193:CPDITR]2.0.CO;2.