

Spatiotemporal variations in juvenile mortality and cohort strength of Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador

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Abstract: Juvenile mortality is an important factor affecting the spatiotemporal dynamics of fish recruitment, but estimation of the spatiotemporal variations in juvenile mortality rates remains challenging. We developed a state-space metapopulation dynamics model to simultaneously estimate spatiotemporal variations in juvenile mortality rates and cohort strength and applied this general modelling framework to data from multiple surveys for juvenile (ages 2–5) Atlantic cod (*Gadus morhua*) stocks off Newfoundland and Labrador (NL). We found large-scale synchronized dynamics of decreasing juvenile mortality rates and increasing cohort strength from offshore surveys off eastern and southeastern NL, suggesting improving reproduction and survival rates for juvenile cod. No synchronized patterns of juvenile mortality rates and cohort strength were detected for cod stocks off southern and western NL, indicating more complex cod population spatial structures in those areas. Our study demonstrates the potential of juvenile mortality to cause temporally variable and spatially synchronized dynamics of fish recruitment, and the spatial patterns of juvenile mortality and cohort strength indicate some potential mismatch between cod population structure and current management units off NL.

Résumé : Si la mortalité juvénile est un important facteur agissant sur la dynamique spatiotemporelle du recrutement de poissons, l'estimation des variations spatiotemporelles des taux de mortalité juvénile demeure difficile. Nous avons mis au point un modèle d'espace d'états de la dynamique de la métapopulation pour estimer simultanément les variations spatiotemporelles des taux de mortalité juvénile et de l'abondance des cohortes et avons appliqué ce cadre de modélisation général aux données de plusieurs évaluations portant sur des stocks de morues (*Gadus morhua*) juvéniles (de 2 à 5 ans) au large de Terre-Neuve-et-Labrador (T.-N.-L.). Nous relevons une dynamique synchronisée à grande échelle de diminution des taux de mortalité juvénile et d'augmentation de l'abondance des cohortes pour les évaluations au large de l'est et du sud-est de T.-N.-L., ce qui indiquerait une amélioration de la reproduction et des taux de survie des morues juvéniles. Aucun motif synchronisé des taux de mortalité juvénile et de l'abondance des cohortes n'est décelé pour les stocks de morues au large du sud et de l'ouest de T.-N.-L., ce qui témoigne de structures spatiales plus complexes des populations de morues dans ces secteurs. L'étude démontre que la mortalité juvénile pourrait causer une dynamique variable dans le temps et synchronisée dans l'espace du recrutement de poissons, et les motifs spatiaux de mortalité juvénile et d'abondance des cohortes indiquent un mésappariement potentiel entre la structure des populations de morues et les unités de gestion actuelles au large de T.-N.-L. [Traduit par la Rédaction]

Introduction

Two intriguing patterns of fish recruitment are strong temporal variation and large-scale spatial synchronization (e.g., Myers et al. 1997; Houde 2008), and understanding the spatiotemporal dynamics of fish recruitment has been a long-standing challenge in fisheries science. Previous studies on spatiotemporal dynamics of fish recruitment mostly focus on ecological processes during spawning (Brunel 2010; Zhang et al. 2015) and early life-history (e.g., egg, larvae, and early juvenile) stages (Houde 2008), and many theoretical and empirical studies suggest that the strength of fish recruitment is largely determined within the first year of life (Pepin 2016; Zhang et al. 2017). However, for species with a prolonged juvenile stage, juvenile mortality after the first year of life may also have strong effects on the strength of subsequent recruitment. For example, Northeast Arctic cod (*Gadus morhua*) recruitment is affected by juvenile mortality within the first 3 years of life (Bogstad et al. 2016). Both top-down and bottom-up processes may affect fish survival during the juvenile stage. For example, predation on

juvenile flatfish may generate additional variability of fish recruitment (Bailey 1994), and feeding success and growth rate of juvenile fish are critical to subsequent recruitment to the fishery (Le Pape and Bonhommeau 2015). Furthermore, synchronized fish recruitment dynamics may be caused by spatially consistent variations of juvenile mortality, if the ecological and (or) anthropogenic factors affecting juvenile mortality act across large spatial scales (Kelly et al. 2009; Frank et al. 2016). However, to our knowledge, few empirical studies have examined the effects of juvenile mortality on the spatiotemporal variations of fish recruitment.

Atlantic cod off Newfoundland and Labrador (NL) are managed as four separate stocks: (1) northeastern Newfoundland – southern Labrador (northern) cod, (2) southern Grand Bank cod, (3) southern Newfoundland cod, and (4) northern Gulf of St. Lawrence cod. Cod on the Flemish Cap, just outside of Canada's 200 mile (1 nautical mile = 1.852 km) exclusive economic zone (EEZ), are also managed as a separate stock. The NL and Flemish Cap cod stocks are delineated by Northwest Atlantic Fisheries Organization

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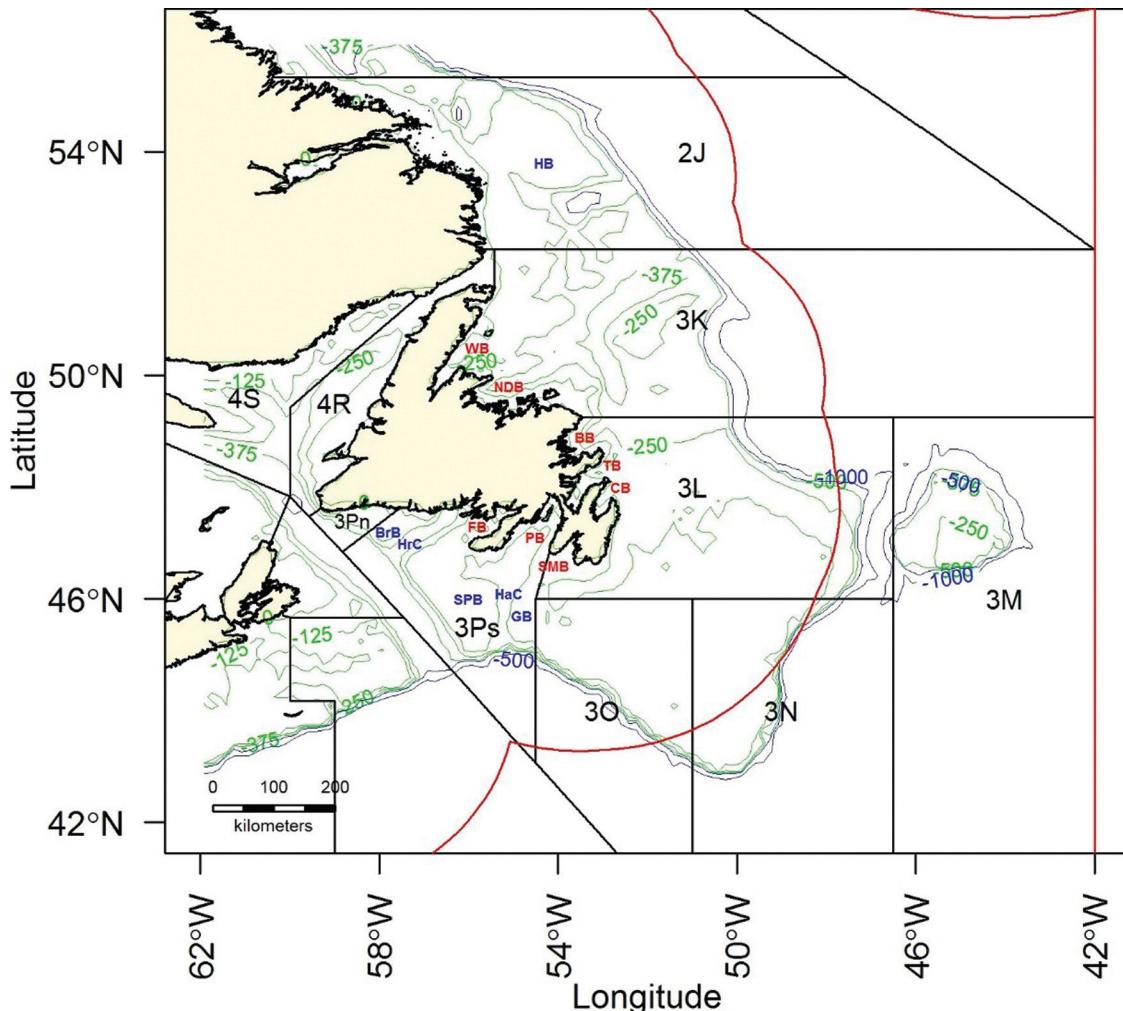
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Fig. 1. Study area and fisheries management divisions of Northwest Atlantic Fisheries Organization (NAFO). Map is drawn by PBSmapping package in R (Schnute et al. 2019) using depth data from Fisheries and Oceans Canada and management division boundary data from NAFO. [Colour online.]

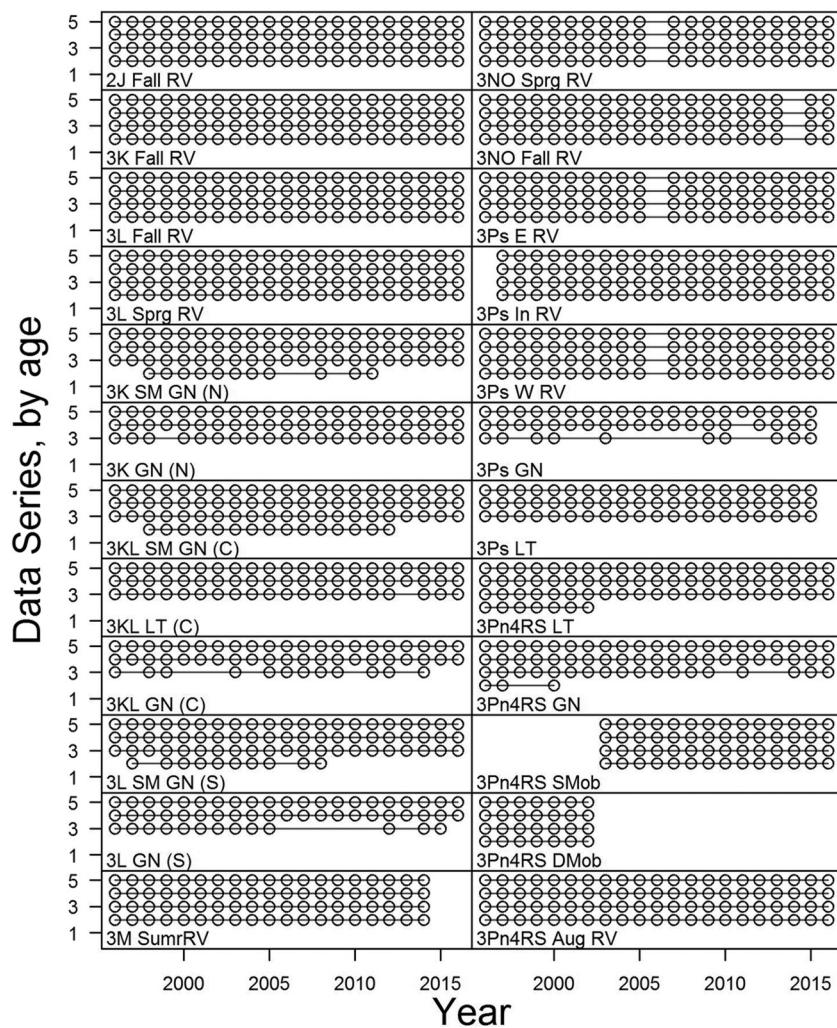


(NAFO) divisions (Fig. 1). Boundaries for these divisions were primarily set according to cod and haddock (*Melanogrammus aeglefinus*) distributions that dominated the Northwest Atlantic fishery when subdivisions were first proposed for these regions (Halliday and Pinhorn 1990). The stock boundaries are as follows: (1) northern cod, 2J3KL; (2) southern Grand Bank cod, 3NO; (3) southern Newfoundland cod, 3Ps; (4) northern Gulf of St. Lawrence cod, 3Pn4RS; and (5) Flemish Cap, 3M. There is evidence that the spatial distribution of cod within at least some of these populations has changed over the past few decades. For example, large aggregations of cod off the northeast coast of Newfoundland were concentrated inshore in the 1990s, which is contrary to historical patterns (Bradbury et al. 2008). However, the division boundaries used to delineate cod stocks around NL have remained relatively unchanged since the NAFO convention in 1979 (Halliday and Pinhorn 1990). An improved understanding of spatiotemporal variation in juvenile mortality and cohort strength may lead to better understanding of population structure and inform the spatial management of NL cod fisheries (e.g., Goethel and Berger 2017).

In this paper, we develop a metapopulation dynamics model in a state-space framework that includes autocorrelated juvenile mortality rates and cohort strength that are also correlated across surveys in an unstructured manner. This is an extension to previous methods used to estimate juvenile mortality rates (Myers and

Cadigan 1993a; Fromentin et al. 2001; Gudmundsson 2004), which can be used to explore the covariation indicated by the age-based indices of juvenile abundance. Myers and Cadigan (1993a) and Fromentin et al. (2001) proposed single population models for juvenile survey indices (ages 0 and 1) that included a density-dependent component for natural mortality and also random density-independent mortality effects to account for other year-to-year variations in mortality. We extend on their models by including many juvenile surveys and correlations between metapopulations, more juvenile ages, and time-series correlations in cohort strength and juvenile mortality rates. We do not include density-dependent effects in our model, although this would be a straightforward modelling extension. However, we do investigate density-dependent effects in our model results. Our basic model is more similar to the one proposed by Gudmundsson (2004), but we extend it for multiple metapopulation surveys and include autocorrelation in juvenile mortality rates and cohort strength.

We apply our model to Atlantic cod stocks off NL, using 24 time series of juvenile (ages 2–5) abundance indices from surveys across spatial regions off NL and including the Flemish Cap (Fig. 2). Tulk et al. (2017) recently investigated spatiotemporal variations in recruitment, but not juvenile mortality rates, for the same surveys. We extend and improve the modelling approach of Tulk et al. (2017) in several aspects. In particular, our model includes variation in juvenile mortality rates, which the model in Tulk

Fig. 2. Data summary of the 24 survey indices.

[et al. \(2017\)](#) did not, and this can have important impacts on estimating cohort strength. We also estimate correlations between metapopulations within our model, whereas [Tulk et al. \(2017\)](#) estimated metapopulation correlations in cohort strength from single population model outputs. Our correlation modelling approach is more similar to that of [Minto et al. \(2014\)](#), which investigated autocorrelation, and between-stock correlation, in the maximum reproductive rate in stock-recruitment models for many Atlantic cod populations. In contrast with [Minto et al. \(2014\)](#), we focus on juvenile mortality rates and year class strength of NL metapopulations.

Methods

Metapopulation dynamics model

We develop a metapopulation dynamics model to study the spatiotemporal dynamics of juvenile mortality and cohort strength using multiple survey data. In this modelling framework, we consider fishes sampled by each survey to represent a component of the metapopulation and estimate the juvenile mortality and cohort strength within each survey area. We then infer potential metapopulation structure based on the spatiotemporal correlations of juvenile mortality and cohort strength among survey areas.

We use a simple and common cohort population dynamics model for the unfished juvenile ages; thus, fishing mortality is not

included in the models. The model is similar to, for example, the basic model described in [Gudmundsson \(2004\)](#). The model is

$$(1) \quad N_{a,y} = N_{a-1,y-1} \exp(-M_{a-1,y-1})$$

where $N_{a,y}$ represents stock abundance at age a in year y , and $M_{a,y}$ is the mortality rate. We assume that $M_{a,y}$ can be modelled in terms of age- and year-effects; $M_{a,y} = M_a + \delta_y$, where M_a ($a = 0, \dots, A$) is the overall level of juvenile mortality, and δ_y ($y = 0, \dots, Y$) is the annual deviation in M that we assume is common for all juvenile ages. Parameter identification issues are considered later. [Gudmundsson \(2004\)](#) separated juvenile mortality into a constant age-dependent mortality rate plus random deviations that were uncorrelated across ages and years. We assume δ_y values are the same for all juvenile ages and have a stationary distribution derived from an AR(1) process with correlation parameter φ_δ and stationary variance $\sigma_\delta^2/(1 - \varphi_\delta^2)$:

$$(2) \quad \delta_0 \sim N\left(0, \frac{\sigma_\delta^2}{1 - \varphi_\delta^2}\right), \quad \delta_y | \delta_{y-1} \sim N(\varphi_\delta \delta_{y-1}, \sigma_\delta^2), \quad y = 1, \dots, Y$$

Note that $\delta_y | \delta_{y-1}$ denotes the distribution of δ_y conditional on the value of δ_{y-1} , and $\sigma_\delta^2 = \text{Var}(\delta_y | \delta_{y-1}) \leq \text{Var}(\delta_y)$. Let $c = y - a$ indicate

the cohort, and let $n_{a,y} = \log(N_{a,y})$. One can show through recursive applications of eq. 1 that

$$(3) \quad n_{a,c} = n_{0,c} - \sum_{i=0}^{a-1} (M_i + \delta_{c+i}), \quad a > 0$$

which is basically the same as eq. 4 in Gudmundsson (2004). We model $n_{0,c} = n_0 + \gamma_c$ where γ_c is an AR(1) process similar to δ_y :

$$(4) \quad \gamma_0 \sim N\left(0, \frac{\sigma_\gamma^2}{1 - \varphi_\gamma^2}\right), \quad \gamma_c | \gamma_{c-1} \sim N(\varphi_\gamma \gamma_{c-1}, \sigma_\gamma^2), \quad c = 1, \dots, C$$

Let $I_{s,a,y}$ denote the index from survey s , age a , and cohort y . Each age class is assumed to have different catchability, $Q_{s,a}$, which is a product of gear selectivity and availability of fish to the survey. The survey observation equation is

$$(5) \quad I_{s,a,y} = Q_{s,a} N_{s,a,y} \exp[-f_s(M_{s,a} + \delta_{s,y})] \exp(\tau_{s,y} + \varepsilon_{s,a,y})$$

where $\tau_{s,y} \sim \text{N}(0, \sigma_{s,\tau}^2)$ and $\varepsilon_{s,a,y} \sim \text{N}(0, \sigma_{s,e}^2)$ are survey measurement error terms, and f_s is the fraction of year that the survey occurred in. The random year effects ($\tau_{s,y}$) allow for survey measurement errors to be correlated within years, which is a common occurrence in the juvenile survey indices we examine (e.g., Myers and Cadigan 1995b). Gudmundsson (2004) used the same correlated survey measurement error model (see his eq. 14). Fromentin et al. (2001) also included within-year correlated measurement errors for their age 0 and age 1 survey indices. Note that we model population size ($N_{s,a,y}$) separately (but with between-survey correlations in cohort strength) for each survey, and this is one reason why it is important to estimate $\sigma_{s,\tau}^2$ and $\sigma_{s,e}^2$ by survey. However, the autocorrelation parameters for cohort strength (φ_γ) and M deviations (φ_δ) are difficult to estimate with the relatively short survey time series we study. This problem has been noted by others (e.g., Johnson et al. 2016). We address this problem by assuming these correlations are the same for all surveys, thereby increasing the amount of information available to estimate these parameters. Letting $\text{ind}_{s,a,y} = \log(I_{s,a,y})$, and $q_{s,a} = \log(Q_{s,a})$, the statistical expectation of $\text{ind}_{s,a,y}$ conditional on the M deviations (δ values) is

$$(6) \quad E(\text{ind}_{s,a,c} | \delta) = q_{s,a} + n_{s,0,c} - \sum_{i=0}^{a-1} (M_{s,i} + \delta_{s,c+i}) - f_s M_{s,a} - f_s \delta_{s,c+a}$$

The M and Q parameters are confounded, as noted by Myers and Cadigan (1993a) and Gudmundsson (2004), and we cannot directly estimate M values using only survey indices without additional information on the age dependencies in Q values. It is not appropriate to assume Q values are constant over the juvenile ages in our study. However, it is possible to estimate temporal changes in M values (i.e., δ values) if Q values are constant over years even if they are age-dependent. Let $q_{s,a}^* = q_{s,a} - \sum_{i=0}^{a-1} M_{s,i} - f_s M_{s,a}$. Equation 6 is equivalent to

$$(7) \quad E(\text{ind}_{s,a,c}) = q_{s,a}^* + n_{s,0,c} - \sum_{i=0}^{a-1} \delta_{s,c+i} - f_s \delta_{s,c+a}, \quad a > 0$$

and $E(\text{ind}_{s,0,c}) = q_{s,0}^* + n_{s,0,c} - f_s \delta_{s,c}$. The overall scale of $n_{s,0,c}$ is still confounded with the scale of $q_{s,a}^*$ in eq. 7. To remove this confounding, we constrained $q_{s,a}^*$ at age 5 to be zero for each survey, which was the same procedure used by Tulk et al. (2017). Therefore, the scale of the estimates of cohort size provided by the exponent of eq. 7 is the same as the scale of the survey index at age 5. However,

Table 1. Definitions of model random effects, parameters, and other notations.

Symbol	Definition	Dimension
Random effects		
δ_y	Year effect in juvenile mortality	576
γ_c	Cohort effect	576
$\tau_{s,y}$	Survey index year effects	474
$\varepsilon_{s,a,y}$	Index measurement error	1680
Parameters		
$Q_{s,a}$	Survey catchability	66
$q_{s,a}$	$\log(Q_{s,a})$	—
$q_{s,a}^*$	$q_{s,a} - \sum_{i=0}^{a-1} M_{s,i} - f_s M_{s,a}$	—
$n_{s,0}$	Mean recruitment	24
σ_δ^2	$\text{Var}(\delta_y \delta_{y-1})$	24
φ_δ	$\text{Corr}(\delta_y, \delta_{y-1})$	1
σ_γ^2	$\text{Var}(\gamma_c \gamma_{c-1})$	24
φ_γ	$\text{Corr}(\gamma_c, \gamma_{c-1})$	1
$\sigma_{s,\tau}^2$	$\text{Var}(\tau_{s,y})$	24
$\sigma_{s,e}^2$	$\text{Var}(\varepsilon_{s,a,y})$	24
$\rho_{i,j,\delta}$	Correlation coefficient of juvenile mortality between surveys i and j	276
$\rho_{i,j,\gamma}$	Correlation coefficient of cohort strength between surveys i and j	276
Other model notation		
a	Age	
y	Year	
c	Cohort, $y - a$	
s	Survey	
$N_{a,y}$	Stock abundance at age a in year y	
$M_{a,y}$	Mortality rate at age a in year y	
M_a	Mean mortality rate at age a for all years	
$n_{a,y}$	$\log(N_{a,y})$	
$n_{0,c}$	\log cohort size, $n_{0,c} = n_0 + \gamma_c$	
$I_{s,a,c}$	Index from survey s , age a , and cohort c	
$\text{ind}_{s,a,c}$	$\log(I_{s,a,c})$	
f_s	Fraction of year that the survey occurred in $S \times 1$ vector with sth element $\delta_{s,y} - \varphi_\delta \delta_{s,y-1}$	
$\Delta_{\delta,y}$	$\text{Cov}(\Delta_{\delta,y})$, which is the same each year	
Σ_δ	$S \times 1$ vector with sth element $\gamma_c - \varphi_\gamma \gamma_{c-1}$	
$\Delta_{\gamma,y}$	$\text{Cov}(\Delta_{\gamma,y})$, which is the same each year	
Σ_γ		

this constraint has no effect on the log cohort size deviations from the mean for all years, and it is these deviations that we need to estimate the correlation in cohort size from any two surveys. Similarly, we can directly estimate the correlation in the log of $M_{s,a,y}$ for two surveys.

Both $M_{s,a,y}$ and $n_{s,0,c}$ are derived from AR(1) processes and we include between-survey correlation in the AR(1) deviations. Let $\Delta_{\delta,y}$ be the $S \times 1$ vector of AR(1) deviations for all of the surveys, with sth element $\delta_{s,y} - \varphi_\delta \delta_{s,y-1}$, $s = 1, \dots, S$. We assume $\Delta_{\delta,y} \sim \text{MVN}(0, \Sigma_\delta)$, where MVN indicates a multivariate normal distribution with unstructured 24×24 covariance matrix Σ_δ . Since $S = 24$, there are $24 \sigma_{s,\delta}^2$ variance parameters and $24 \times 23/2 = 276$ correlation parameters (i.e., $\rho_{i,j,\delta}$ for correlation between surveys i and j) involved in Σ_δ . For the first year, $\Delta_{\delta,0} = (\delta_{1,0}, \dots, \delta_{S,0})$, and we use the stationary variances to derive Σ_δ . Similarly, let $\Delta_{\gamma,y}$ be the vector of log cohort strength AR(1) deviations with sth element $\gamma_c - \varphi_\gamma \gamma_{c-1}$. We assume $\Delta_{\gamma,y} \sim \text{MVN}(0, \Sigma_\gamma)$ and denote $\rho_{i,j,\gamma}$ as the $[i, j]$ element of Σ_γ .

Model fitting

The statistical model defined above involves many (i.e., 740) fixed effect parameters (see Table 1) for the ages and cohorts within the 24 surveys we investigate. Let $\boldsymbol{\theta}$ be a vector of all fixed effect parameters. The model also involves many random effects: $\{\delta_{s,y}, \gamma_c, \tau_{s,y}, \varepsilon_{s,a,y}\}$. The ε error terms are typical iid observation

Table 2. The full name and abbreviations of 24 survey indices.

Survey	Abbreviation
Fall bottom trawl offshore survey in 2J	2J Fall RV
Fall bottom trawl offshore survey in 3K	3K Fall RV
Fall bottom trawl offshore survey in 3L	3L Fall RV
Spring bottom trawl offshore survey in 3L	3L Sprg RV
Small mesh gillnet inshore survey in 3K	3K SM GN (N)
Gillnet inshore survey in 3K	3K GN (N)
Small mesh gillnet inshore survey in 3KL	3KL SM GN (C)
Line-trawl inshore survey in 3KL	3KL LT (C)
Gillnet inshore survey in 3KL	3KL GN (C)
Small mesh gillnet inshore survey in 3L	3L SM GN (S)
Gillnet inshore survey in 3L	3L GN (S)
Summer bottom trawl offshore survey in 3M	3M Sumr RV
Spring bottom trawl offshore survey in 3NO	3NO Sprg RV
Fall bottom trawl offshore survey in 3NO	3NO Fall RV
Bottom trawl offshore survey in eastern 3Ps	3Ps E RV
Bottom trawl inshore survey in 3Ps	3Ps In RV
Bottom trawl offshore survey in western 3Ps	3Ps W RV
Gillnet inshore survey in 3Ps	3Ps GN
Line-trawl inshore survey in 3Ps	3Ps LT
Line-trawl inshore survey in 3Pn4RS	3Pn4RS LT
Gillnet inshore survey in 3Pn4RS	3Pn4RS GN
Shallow-water bottom trawl inshore survey in 3Pn4RS	3Pn4RS Smob
Deepwater bottom trawl inshore survey in 3Pn4RS	3Pn4RS Dmob
August bottom trawl offshore survey in 3Pn4RS	3Pn4RS Aug RV

errors that, conditional on the δ , γ , and τ random effects, induces a normal distribution on $\text{ind}_{s,a,y}$ (see eq. 5). We use marginal maximum likelihood for parameter estimation and statistical inference about θ , based on the marginal distribution of $\text{ind}_{s,a,y}$. This involves integrating out the δ , γ , and τ random effects from the joint density function of all $\{\text{ind}_{s,a,y}\}$ and $\{\delta_{s,y}, \gamma_{s,y}, \tau_{s,y}\}$. This approach is described in more detail in Skaug and Fournier (2006). We use the Template Model Builder (TMB) package within R (Kristensen et al. 2016) to evaluate the marginal log-likelihood for θ : $l(\theta)$. The random effects can be predicted by maximizing the joint log-likelihood. TMB also provides the gradient function, $\partial l(\theta)/\partial \theta$, by using automatic differentiation. The gradient function greatly improves parameter estimation using a derivative-based optimizer. We use the nlmrb function within R (Gay 1990) to find the MLE for θ .

Model assumptions are evaluated through detailed examination of model predictions (e.g., year effects) and survey index residuals (see online Supplementary Material¹). Additionally, the reliability of estimates of temporal variations in juvenile mortality rates and cohort strength is assessed using simulation analyses (see online Supplementary Material¹), and this simulation-based efficacy test is another contribution of this paper to previous studies (Myers and Cadigan 1993a; Fromentin et al. 2001; Gudmundsson 2004).

Survey data

We used 24 relative abundance indices of juvenile cod from offshore mobile bottom trawl surveys and inshore fixed gear (i.e., gillnet and line-trawl) surveys (Table 2). Tulk et al. (2017) described the basic methods used to compute stock size indices from these surveys. However, unlike Tulk et al. (2017), we restricted our attention to surveys conducted since 1996. Offshore surveys before the summer of 1995 used a different trawl that had a much different mesh size and did not sample small fish nearly as well as the currently used Campelen 1800 survey trawl (Dempsey et al. 2017). The inshore fixed gear surveys also started in 1995, and selecting survey years after 1995 means that we used a more consistent time

frame for all indices. The estimated age at which 50% of female cod become sexually mature in this region is between 5 and 6 years of age (DFO 2018a, 2018b), and we therefore focused on fish of ages 2–5 as juveniles. We did not use age 1 survey indices because cod at this age were hardly selected in inshore fixed gear surveys and indices were not computed at this age. Also, the catchability of age 1 cod in offshore surveys can be quite variable, because, at this age, much of the stock has a shoreward distribution that was not covered well by the offshore northern and southern cod stock surveys (Anderson and Gregory 2000; Lilly et al. 2000). Hence, restricting our analyses to ages 2–5 means that we have a more consistent set of ages and years for each survey index, and our results indicate population dynamics at ages 2–5 during 1996–2015 (Fig. 2). Surveys were not completed in some years, which is why there are occasional bands of missing values (Fig. 2). Any indices with zero values, or very small values (i.e., $< e^{-5}$), were also not used because of the log-transformation in our cohort model (described below) and the sensitivity of model estimates to these values.

Results

Spatiotemporal variation of juvenile mortality

Predictions of deviations in juvenile mortality for each survey and 95% prediction intervals are provided in the online Supplementary Material (Fig. A1¹). Significant spatial correlations in juvenile mortality were inferred from the 24 survey indices (Fig. 3). These correlations can be classified into two groups: (i) positive correlations among offshore survey indices (2J Fall RV and 3K Fall RV) off eastern NL (NAFO divisions 2J3K) and inshore survey indices (3K GN, 3K SM GN, 3KL GN, 3KL LT, and 3Pn4RS LT) in eastern and western NL (NAFO divisions 3KL and 3Pn4RS); and (ii) positive correlations among offshore surveys (3L Fall RV, 3L Sprg RV, 3NO Fall RV, 3NO Sprg RV) of southeastern NL (NAFO divisions 3LNO) and inshore survey (3Ps In RV) off southern NL (NAFO divisions 3Ps).

The juvenile mortality derived from offshore surveys off eastern NL and inshore surveys off eastern and western NL exhibited an overall decreasing trend from 1993 to 2016 (Fig. 4). Consistently, the juvenile mortality derived from offshore surveys off southeastern NL and inshore survey off southern NL decreased over time, but with a notable cyclic pattern (Fig. 5). The periodicity of the cyclic pattern is around 7 years (Fig. 6).

Spatiotemporal variations of cohort strength among surveys

Predictions of deviations in cohort strength for each survey and 95% prediction intervals are provided in the online Supplementary Material (Fig. A2¹). The spatial correlations of cohort strength among 24 survey indices can be classified into four groups (Fig. 7): (i) positive correlations among offshore surveys (2J Fall RV, 3K Fall RV, 3L Fall RV, 3L Sprg RV, 3NO Fall RV, 3NO Sprg RV, and 3Ps E RV) off eastern and southeastern NL (NAFO divisions 2J3KLNOPs); (ii) positive correlations among surveys (3Ps In RV, 3Pn4RS Aug RV, and 3Pn4RS SMob) off southern and western NL (NAFO divisions 3Ps and 3Pn4RS); (iii) positive correlations among inshore surveys (3K GN, 3K SM GN, 3KL GN, 3KL LT, 3KL SM GN, and 3L GN) off eastern NL; and (iv) positive correlations between line-trawl surveys (3Ps LT and 3Pn4RS LT) off southern and western NL.

The cohort strength derived from offshore surveys off eastern and southeastern NL increased over time with strong temporal variations (Fig. 8a). The cohort strength derived from inshore surveys off southern and western NL remained relatively constant over time, with a slight increase in recent years (Fig. 8b). The cohort strength derived from inshore surveys off eastern NL decreased over time, but then increased since 2010 (Fig. 8c). The

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0156>.

Fig. 3. Spatial correlations of deviations of juvenile M values derived from 24 survey indices. Blue circles are positive correlations, and red circles are negative correlations. One star means barely significant correlation ($P < 0.05$), two stars mean significant correlation ($P < 0.01$), and three stars mean very significant correlation ($P < 0.001$). [Colour online.]

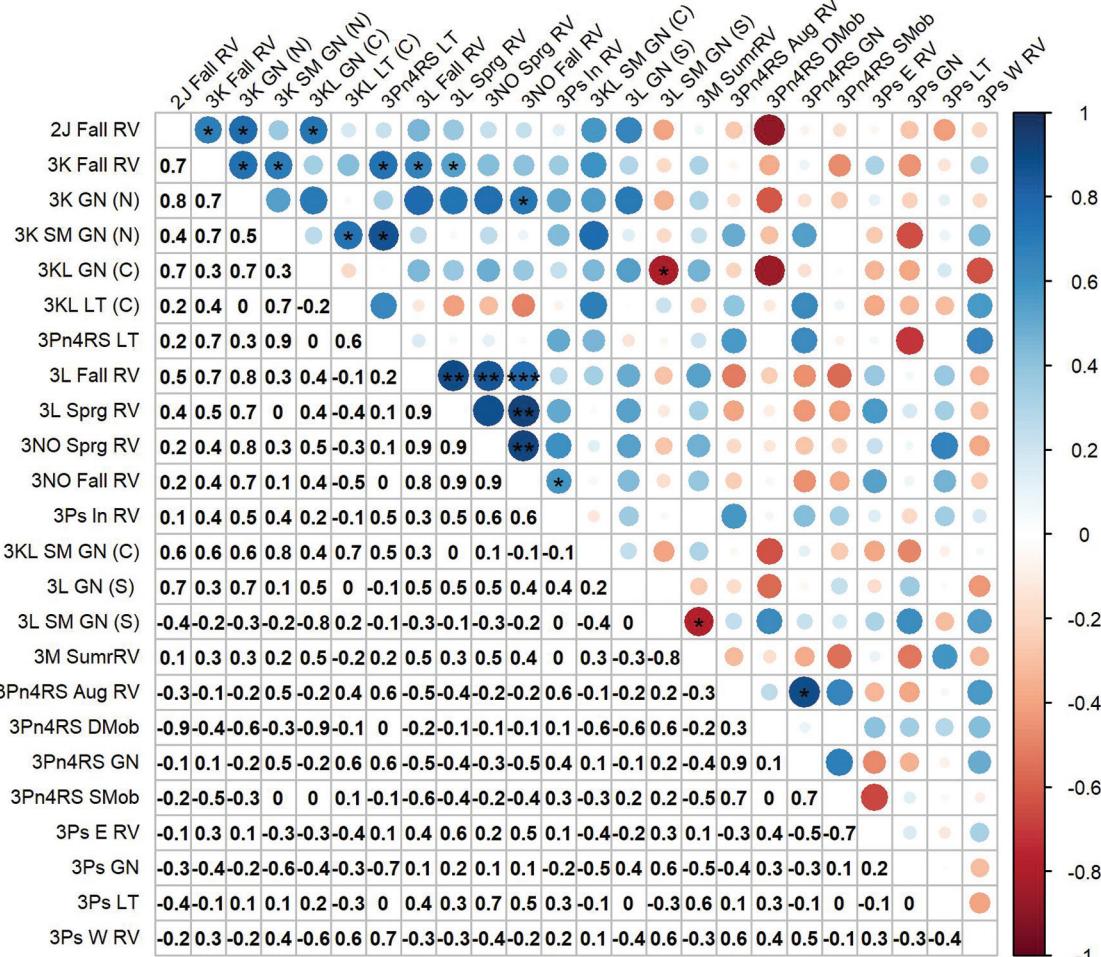


Fig. 4. Temporal variation of the deviations of juvenile M values derived from offshore survey indices in 2J3K (2J Fall RV and 3K Fall RV) and inshore survey indices in 3KL and 3Pn4RS (3K GN, 3K SM GN, 3KL GN, 3KL LT, and 3Pn4RS LT). [Colour online.]

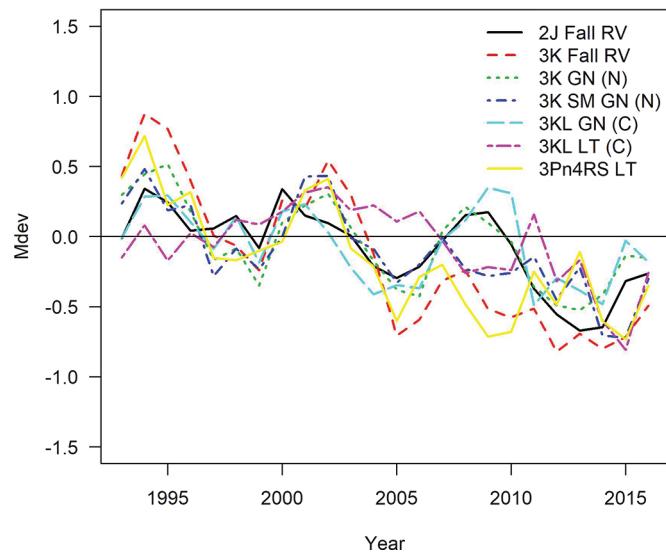


Fig. 5. Temporal variation of the deviations of juvenile M values derived from offshore surveys in 3LNO (3L Fall RV, 3L Sprg RV, 3NO Fall RV, 3NO Sprg RV) and inshore survey in 3Ps (3Ps In RV). [Colour online.]

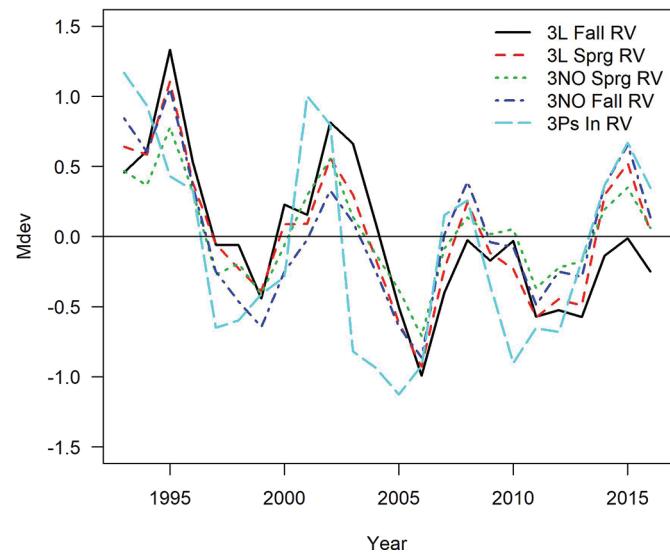
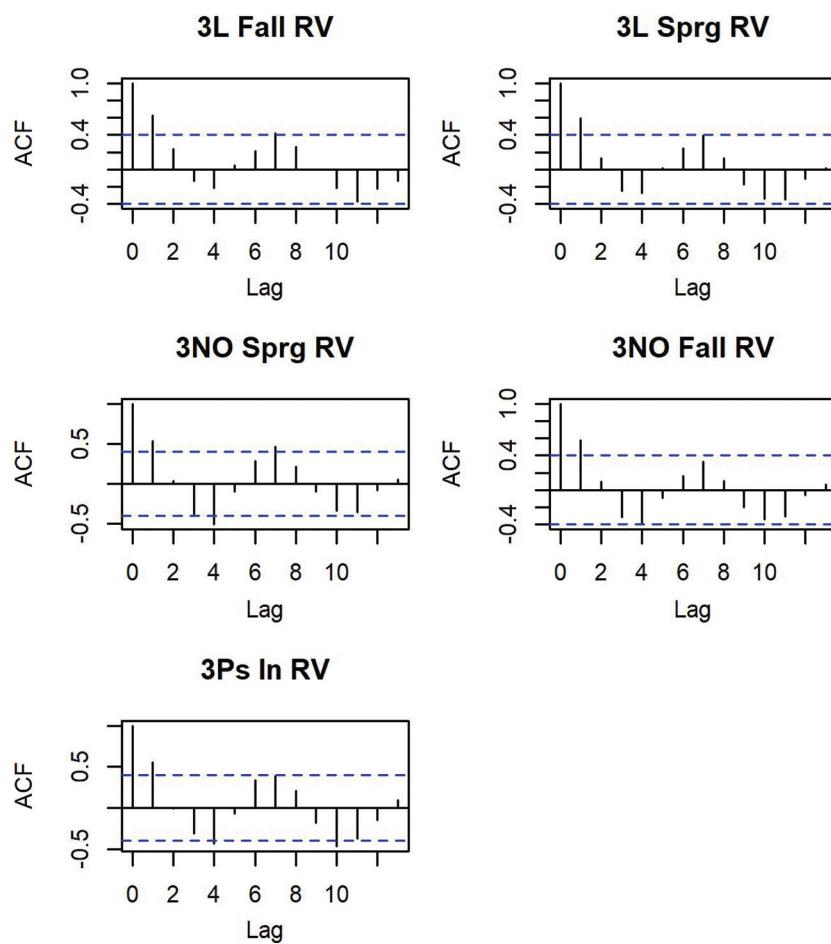


Fig. 6. Autocorrelation of deviations of juvenile M values derived from offshore surveys in 3LNO (3L Fall RV, 3L Sprg RV, 3NO Fall RV, 3NO Sprg RV) and inshore survey in 3Ps (3Ps In RV). [Colour online.]



cohort strength derived from line-trawl surveys off southern and western NL also decreased over time (Fig. 8d) and have not shown any recent reversal in this trend.

Discussion

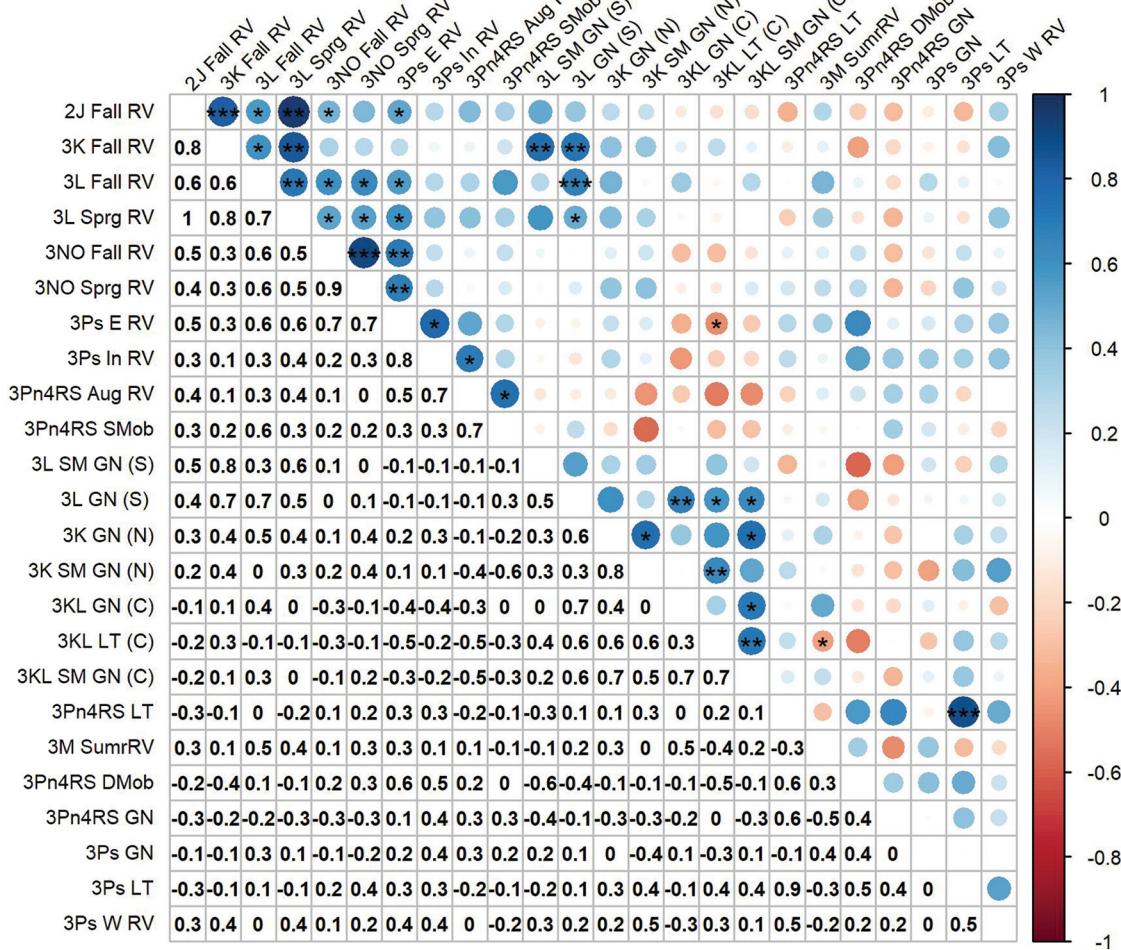
Estimation of juvenile mortality and cohort strength

We developed a cohort model to describe juvenile population dynamics, including variation in cohort strength and natural mortality rates. This modelling framework allows us to identify spatiotemporal correlations among population components in a region, which would help to delineate stock structure. The main relevance of focusing on juveniles is that we assume they are not commercially exploited. Otherwise the catch information should be integrated into the model and one is then basically doing a full stock assessment. The basic model (eq. 7) is appropriate and can be applied to any stock where a time series of age-based survey indices of abundance are available. We also extended our model in a metapopulation context, and the model can be applied in any situation where there are sets of age-based juvenile survey abundance indices available. The core of the TMB model code is short and concise, which could easily be adapted and applied to alternate species or data situations with TMB software.

Tulk et al. (2017) analyzed the same surveys using a simple cohort strength model and then estimated between-survey correlations in their estimates of cohort strength. We extend and improve on their methods in four main aspects. First, we consider spatiotemporal variation in both cohort strength and juvenile mortality rates, whereas Tulk et al. (2017) assumed juvenile mor-

tality rates were constant over time (although possibly age-dependent), which has implications on the estimation of cohort strength. Second, we estimated between-survey correlations in cohort strength and juvenile mortality rates within the model, whereas Tulk et al. (2017) simply computed the correlations based on estimates of cohort strength for each survey. Their approach does not account for different uncertainties in cohort strength estimates at the start and end of a time series when there are fewer ages used to derive the estimates or for the different uncertainties between estimates of cohort strength from different surveys. Our modelling approach better accounts for these uncertainties. Third, we model survey year effect variance parameters separately for each survey because the magnitude of year effect variation is not the same for all surveys. We examined the model predictions of year effects closely (e.g., Fig. A5 in Supplementary Material¹) to assess whether they were confounded with cohort deviations. We only found year effects for 10 of 24 surveys, and in this case the year effects varied without trend and did not seem to be confounded with changes in cohort strength. Tulk et al. (2017) included year effects that were common to all surveys, and there is a strong potential that their year effects were confounded with their cohort effects, which could lead to biased results. Fourth, we model residual variance parameters separately for each survey, which is important when there are model parameters that are common to multiple surveys, and unaccounted residual heterogeneity may have a large effect on model fit statistics (e.g., AIC) for model selection.

Fig. 7. Spatial correlations of deviations of cohort strength derived from 24 survey indices. Blue circles are positive correlations, and red circles are negative correlations. One star means barely significant correlation ($P < 0.05$), two stars mean significant correlation ($P < 0.01$), and three stars mean very significant correlation ($P < 0.001$). [Colour online.]



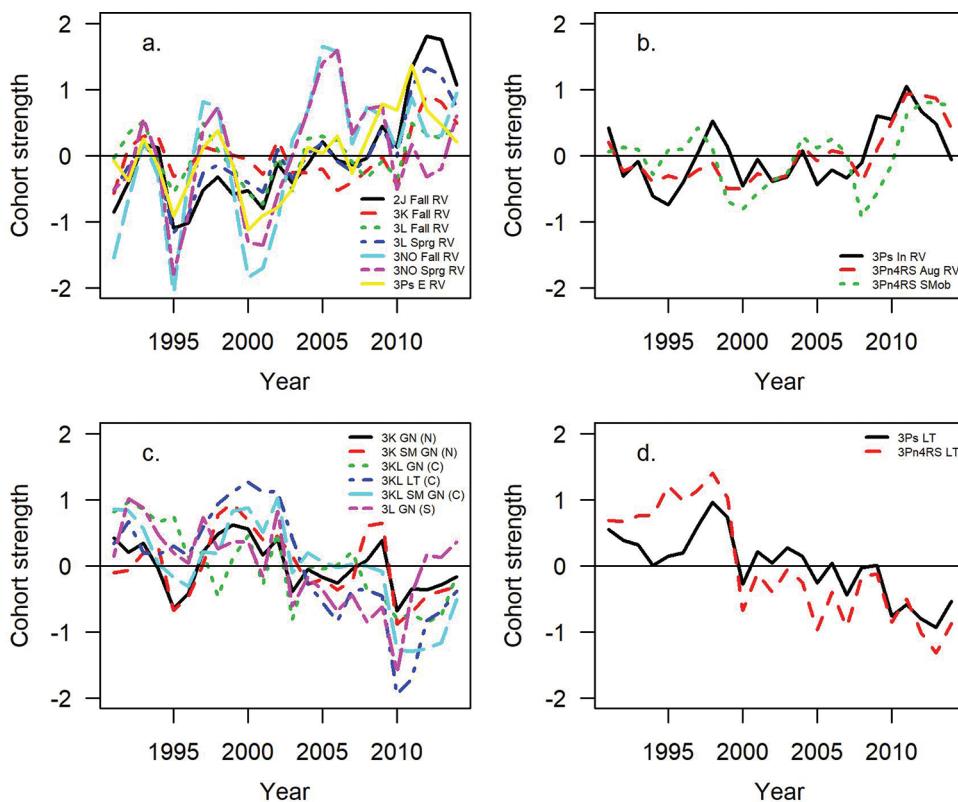
The model we propose is similar to that in Gudmundsson (2004) and to a lesser extent to models proposed by Myers and Cadigan (1993a) and Fromentin et al. (2001). However, unlike Gudmundsson (2004), our model (i) does not require stock assessment model estimates of recruitment and (ii) has been implemented in TMB and is estimated using a standard marginal maximum likelihood method, and (iii) we simulation-tested our model estimation and found satisfactory results. We simulation-tested the model (Supplementary Material¹), including a scenario where there were only two juvenile ages and a 20-year time series and found that estimation errors of deviations in cohort strength and natural mortality rates were relatively small even under this worst case scenario. Estimation errors were smaller when more juvenile ages were used in the model or when the length of the abundance index time series was longer. Additionally, estimation of deviations in cohort strength were more accurate in simulation scenarios in which the natural mortality rate changed and were still relatively accurate even in the scenario when the natural mortality rate was constant.

Fish recruitment and juvenile mortality

Fish mortality during the juvenile stage, although perhaps not as well recognized as mortality during earlier life stages, may also affect the strength of recruitment (Myers and Cadigan 1993b; Lough 2010; Bogstad et al. 2016). We detected significant temporal variations of juvenile mortality of Atlantic cod off NL. Among

offshore RV surveys in eastern and southeastern NL, the spatially synchronized decrease of juvenile mortality coincided with increased cohort strength (age 2 cod abundance) that was also spatially correlated. Myers and Cadigan (1993b) detected strong density-dependent juvenile mortality for Atlantic cod at ages 0–2 (i.e., juvenile mortality increased with increasing juvenile abundance). However, we detected a different pattern for juvenile cod ages 2–5, where juvenile mortality actually decreased with increasing juvenile abundance. Positive links between density and survival have previously been suggested for schooling fish, where increased numbers of schooling individuals may provide a fitness benefit in terms of prey detection as well as predator detection and avoidance (Pitcher et al. 1982; Landa 1998; Bertrand et al. 2006). Brattey et al. (2018) also indicated a recent decrease in juvenile mortality rates for northern cod (NAFO divisions 2J3KL), suggesting improving survival conditions for juveniles since about 2005. Consistently, the cohort strength of northern cod increased in recent years (Gregory et al. 2018). The most noticeable environmental change in the region in the past decade has been above normal ocean temperatures, with record highs in 2011 (DFO 2018a). While temperature has generally been dismissed in favour of overfishing as a causative factor in the collapse of the northern cod stock in the late 1980s to early 1990s (Hutchings and Myers 1994; Myers and Cadigan 1995a; Hutchings 1996), increasing temperatures are believed to have played a role in the recovery of

Fig. 8. Temporal trends of the deviations of cohort strength derived from (a) offshore surveys in 2J3KLNOPS (2J Fall RV, 3K Fall RV, 3L Fall RV, 3L Sprg RV, 3NO Fall RV, 3NO Sprg RV, and 3Ps E RV); (b) surveys in 3Ps (3Ps In RV) and 3Pn4RS (3Pn4RS Aug RV and 3Pn4RS SMob); (c) inshore surveys in 3KL (3K GN, 3K SM GN, 3KL GN, 3KL LT, 3KL SM GN, and 3L GN); and (d) line-trawl surveys in 3Ps and 3Pn4RS (3Ps LT and 3Pn4RS LT). [Colour online.]



Barents Sea cod via an increase in the extent of suitable feeding areas (Kjesbu et al. 2014). There is no evidence, however, that feeding conditions for northern cod have improved, with both capelin (*Mallotus villosus*) and northern shrimp (*Pandalus borealis*) stocks at low levels and general declining trends in primary production and zooplankton abundance (DFO 2018a). While harp seals (*Pagophilus groenlandicus*) in this area are currently highly abundant, the cod population is thought to be controlled by bottom-up processes rather than top-down predation by seals (Buren et al. 2014). It should be noted, however, that changes in the distribution of the cod stock may also influence predator-prey interactions with higher and lower trophic levels. Further studies are needed to explore possible mechanisms causing decreasing juvenile natural mortality of cod stocks off eastern and southeastern NL.

In our study, cyclic variations of juvenile mortality are detected among bottom trawl offshore surveys off eastern and southeastern NL, suggesting strong effects of periodic ecological processes on the survival of juvenile cod. This intriguing pattern may be attributed to periodic variations of environmental factors (e.g., North Atlantic Oscillation) or cyclic dynamics of predation (e.g., cannibalism). Effects of climate change on fish recruitment were well documented, which were mostly via ecological interactions in egg and larvae stages (Stige et al. 2006; Ludsin et al. 2014). Nevertheless, the potential effects of climate change on fish juvenile mortality were largely dismissed. Predation, including cannibalism, is an important factor affecting juvenile mortality (Bailey 1994), especially for Atlantic cod (Longhurst 2008; Bogstad et al. 2016). Cannibalism was found to be able to cause cyclic dynamics of fish populations (Sanderson et al. 1999). For Atlantic cod, negative autocorrelations of recruitment with lag of 3–5 years (period of 6–10 years) were detected, suggesting effects of cannibalism

and (or) intraspecific competition at high population levels (Ricard et al. 2016). Further analysis is needed to test whether and how cannibalism may lead to cyclic variations of juvenile mortality.

Another intriguing pattern is that inshore surveys off eastern NL indicated decreasing juvenile mortality and decreasing cohort strength, suggesting density-dependent juvenile mortality in inshore areas. The DFO assessment for northern cod suggests there have been changes in survey catchability, both inshore and offshore. For the combined 2J3KL inshore index, the assessment indicates an overall decreasing pattern in catchability during 1995–2015 (F. Zhang, R. Rideout, N. Cadigan, unpublished data). Additionally, for the combined 2J3KL offshore index, Cadigan (2016) indicated a large change in catchability at ages 5–12 and some change in catchability at ages 2–5. The situation is complicated, but overall we think that possible changes in the overwintering spatial distribution of cod in 2J3KL that may have occurred during 1995–2009 (e.g., Rose et al. 2011), combined with possible changes in inshore survey catchability (possibly due to changes in stock availability to the inshore, or saturation of the gillnets, among other reasons), may be the cause for the change in catchability. These changes in catchability could partly be confounded with the patterns in cohort strength and juvenile mortality we found for surveys in this area. Therefore, the apparent decrease of cohort strength in inshore surveys may be confounded by reduced catchability of inshore surveys.

Population structure of Atlantic cod off NL

Halliday and Pinhorn (1990) documented the establishment and modification of fishery management divisions in the Northwest Atlantic and suggested that the positioning of divisional boundaries was heavily based on knowledge of cod and haddock stock

structure. Despite the fact that these divisional boundaries have changed little since the NAFO convention was established in 1979 (Halliday and Pinhorn 1990), there is much biological evidence that cod stock structure is not as simple as implied by current management boundaries. For example, genetic studies of cod stock structure have produced variable results, with some studies suggesting biological units either smaller than (e.g., Bentzen et al. 1996; Ruzzante et al. 2000; Beacham et al. 2002) or larger than (Pépin and Carr 1993; Lait et al. 2018; Puncher et al. 2019) current management units. Tag–recapture studies have demonstrated some level of (seasonal) spatial overlap between many of the cod stocks examined here (e.g., Brattey et al. 1999; Bérubé and Fréchet 2001). On the other hand, cod also demonstrate strong natal homing and spawning-site fidelity, suggesting the potential for sub-stock structuring at smaller spatial scales (Beacham et al. 2002). There is also evidence for both migratory and nonmigratory components within individual cod stocks (Kirubakaran et al. 2016; Kess et al. 2019). The variable findings of these and other studies clearly indicate that the spatial structure of cod stocks off NL is complicated and currently not fully understood (Smedbol and Wroblewski 2002; DFO 2018b).

Examining correlations in mortality and recruitment among neighboring (or portions of neighboring) cod stocks, as done here, could provide additional insight into the spatial structure of these stocks. Our results generally support current knowledge of fish movements and mixing. For example, the synchronized juvenile mortality and cohort strength observed between neighboring stock management areas such as 3L and 3NO, as well as 3NO and 3Ps, may be indicative of fish movement across these stock boundaries and is supported by mark–recapture studies (e.g., Brattey et al. 1999). Similar to Tulk et al. (2017), neither juvenile mortality nor cohort strength were significantly correlated among inshore and offshore surveys off southern NL, which may support the notion that the cod stock off southern NL is in fact a complex mix of offshore and inshore components (DFO 2018b). Positive correlations of cohort strength detected between surveys off southern NL (i.e., Burgeo Bank) and western NL are consistent with the notion of a substantial seasonal spatial overlap between these two stocks (Méthot et al. 2005). Additionally, the juvenile mortality and cohort strength of cod on the Flemish Cap (NAFO division 3M) was generally not correlated to other areas off NL, which is consistent with the idea that the cod population on the Flemish Cap represents a distinct and isolated stock (Beacham et al. 2002).

Although our results on the spatiotemporal dynamics of juvenile mortality and cohort strength support numerous other studies that suggest a potential mismatch between cod biological population structure and spatial management units, it is important to note that the correlations presented here do not represent irrefutable proof regarding population connectivity. It is possible that such correlations may simply be indicative of large-scale environmental forces acting on species biology and population dynamics at a sufficiently large enough spatial scale to similarly influence multiple stocks (Myers et al. 2015). Additional work is clearly needed to understand the mechanisms causing the observed correlations, so that the biological population structure can be better identified. Additionally, it is necessary to test the effects of any potential mismatch between population structure and management units using scenario simulations, so that the risks of overexploitation or underutilization can be quantified (Kerr et al. 2017).

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