Limited temporal variability in natural mortality for juvenile American plaice on the Grand Bank of Newfoundland

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Abstract

Increases in natural mortality have been suggested as a potential driver for both the collapse and lack of recovery for the American plaice (*Hippoglossoides platessoides*) population on the Grand Bank of Newfoundland in NAFO Divisions 3LNO. However, natural mortality is among the most difficult parameters to estimate since it can be confounded with other parameters and model misspecifications. One method used to avoid this confounding involves modeling unfished components of a population where total mortality and natural mortality are equal. Here, we use a state-space metapopulation dynamics model to investigate whether there is evidence that natural mortality rates for unfished juvenile American plaice have varied since the population collapse. In addition, our model examined the degree of synchrony in age-1 recruitment signals between each management Division. The best fitting model included temporal variability in natural mortality rates, but estimates did not frequently differ from zero. This indicates that change in natural mortality rates is not an important driver of current juvenile 3LNO American plaice stock dynamics. Instead, this model identified that juvenile stock dynamics were mainly affected by variations in age-1 recruitment. Furthermore, a correlation analysis of the temporal variations in recruitment showed that trends were somewhat dissimilar between NAFO Divisions 3L and 3NO. Overall, although increases in M have been suggested by recent studies, we did not find strong evidence for this in juvenile fish.

Keywords: cohort dynamics, population dynamics, recruitment, spatiotemporal, state-space models

Introduction

Increases in natural mortality rates (M's) have been suggested as a potential driver for both the collapse and lack of recovery for the American plaice (*Hippoglossoides platessoides*) population on the Grand Bank of Newfoundland in NAFO Divisions 3LNO (Morgan and Brodie, 2001; COSEWIC, 2009; Morgan *et al.,* 2011; Perreault *et al.,* 2020). In fact, in the most recent run of the ADAPT model for this stock (Wheeland *et al.,* 2021) and in previously accepted models (*e.g.* Wheeland *et al.,* 2018), the assumed M was increased from 0.2 to 0.53 for all ages from 1989 to 1996. In the late 1980s – early 1990s 3LNO American plaice collapsed, and despite a moratorium on directed commercial fishing since 1994, the population has yet to recover (Fig. 1; Wheeland *et al.,* 2021). Despite an expectation that the collapse and lack of recovery were mainly driven by overfishing (directed fish-

ing for the collapse, and bycatch for the lack of recovery), population dynamics models have indicated that known catches are unlikely to account for observed increases in total mortality rates (Z) both during and after the collapse (Morgan and Brodie, 2001; Perreault *et al.,* 2020). Such increases in Z have consequently been, at least partially, attributed to shifts in M. These shifts are hypothesized to be linked to particularly low bottom-water temperatures that covered the Grand Bank during this time-period (Morgan, 1992; Walsh *et al.,* 2004; Robertson *et al.,* 2021); however, direct estimation of the temporal variability in M and its drivers has yet to occur.

Although M is often considered to be one of the most important parameters in a fish stock assessment model, it is also among the most difficult parameters to estimate using commonly available data (Punt *et al.,* 2021). It can be confounded with survey gear selectivity and fishing

mortality rates (Pope *et al.,* 2021). Even when M can be estimated numerically, it may be confounded or aliased with other model misspecifications and M estimates may then be unreliable. There are two main methods capable of avoiding the confounding issue. The first is integration of additional data that can inform M estimates. This usually involves tagging data (*e.g.* Pine, Pollock, Hightower, Kwak, and Rice, 2003; Cadigan, 2015), but there are recent examples that used fish condition indices (*e.g.* Regular *et al.,* 2022). Another approach involves examinations of unfished components of a population (Myers and Cadigan, 1993a, 1993b; Gudmundsson, 2004; Zhang *et al.,* 2020). Although 3LNO American plaice lack a time-series of mark-recapture data (but see Morgan (1996) for a tagging experiment), this stock benefits from having research surveys that catch a wide range of ages, including juvenile age-classes (ages 1–5) that are too small to be captured by the fishery. Survey indices of these age-classes provide a means to examine trends in M for the juvenile component of this population since their Z and M should be equal.

Here we use a state-space metapopulation dynamics model to investigate whether there is evidence that American plaice juvenile M has varied since the population collapse. This model is applied to juvenile (ages 1–5) abundance indices on the Newfoundland Grand Bank since 1995. American plaice have spatiotemporally varying, sexually dimorphic growth with juveniles growing from approximately 5 to 20cm, female maturation occurring around age eight, and male maturation occurring around age four in recent years in NAFO divisions 3LNO (Zheng *et al.*, 2020a, 2020b). A previous use of this model assessed juvenile cod M around Newfoundland and Labrador, where both cohort strength and M were found to vary across space and time (Zhang *et al.,* 2020). Here, we limited our analysis to one stock on the Grand Bank, but allowed for separate estimates in each management division due to previous findings of divisional-level recruitment asynchrony (Kumar *et al.,* 2019).

Materials and Methods

Metapopulation dynamics process model

The model used here was developed by Zhang *et al.* (2020) and a more detailed description can be found there. Briefly, this model framework uses age-based survey indices of
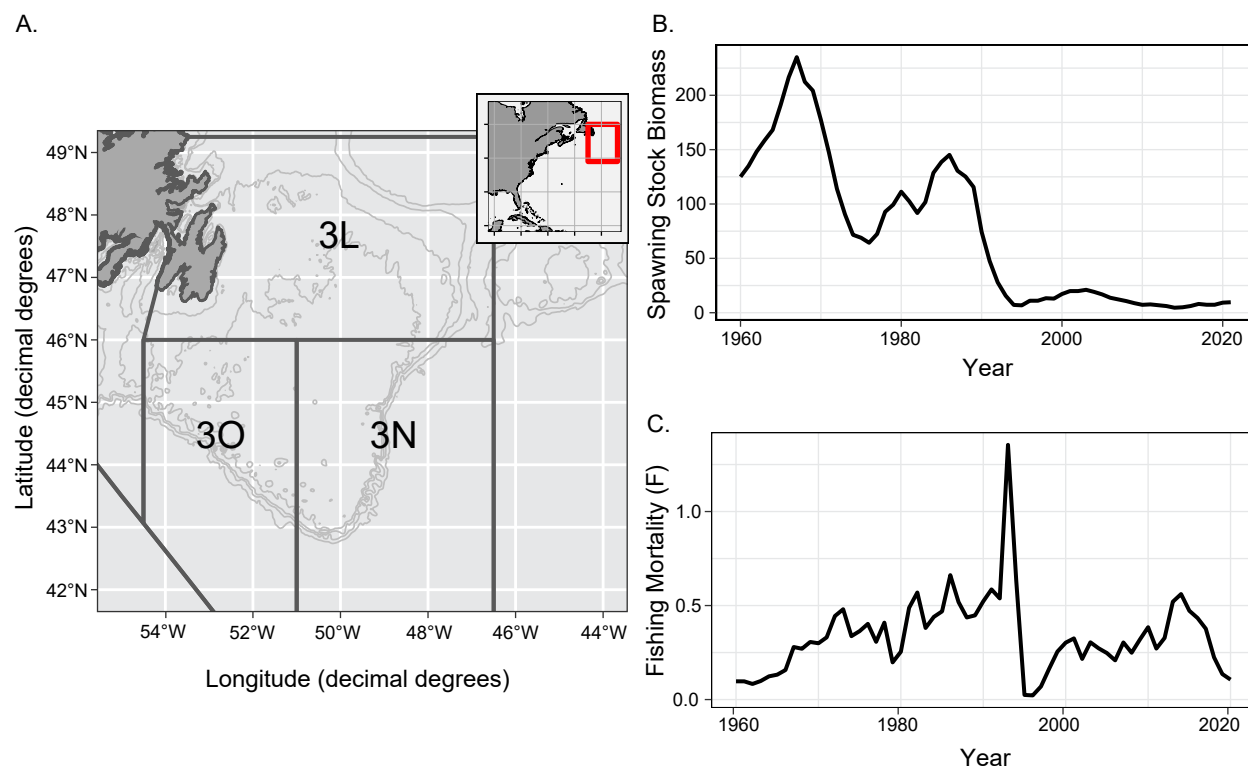

Fig. 1.   Map of NAFO Divisions 3LNO (**A**) and estimates of recent spawning stock biomass (**B**) and fishing mortality (**C**) from the most recent run of the stock assessment model (Wheeland *et al.* 2021). Light grey lines in panel A represent bathymetric contours at 100, 200, 400, and 1000m depth. Spawning stock biomass estimates are in the 1000s of tons and estimates of fishing mortality are the average estimates for ages 9–14.

unfished juvenile fish abundance to estimate changes in juvenile M and cohort strength within metapopulation units. The model is based on the common cohort population model, $N_{a,y} = N_{a-1,y-1}\exp(-M_{a-1,y-1})$, where $N_{a,y}$ represents stock abundance at age a in year y and $M_{a,y}$ is the natural 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 ($a = 0,...,A$) is the overall level of juvenile mortality at age a and δ_y ($y = 0,...,Y$) is the annual deviation $M_{a,y} - M_a$ that we assume is common for all juvenile ages. If $c = y - a$ indicates the cohort and $n_{a,y} = \log(N_{a,y})$, then we can show through recursive applications of the basic cohort model that

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

We model δ_y for $y = 1,...,Y$ using a stationary Gaussian autoregressive process with a correlation parameter φ_δ and stationary variance $\sigma_\delta^2/(1 - \varphi_\delta^2)$:

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

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

In addition, we model the time-series of the initial cohort abundance ($n_{0,c}$; *i.e.* recruits) using an intercept plus a Gaussian autoregressive cohort effect (γ_c),

$$n_{0,c} = n_0 + \gamma_c, \tag{3}$$

where

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

Observation model

Our model is based on bottom trawl research survey indices ($I_{s,a,y}$), where s denotes the survey, a denotes the age, and y denotes the year. Each age-class in the surveys is expected to have unique catchability ($Q_{s,a}$) which is based on gear selectivity and availability of fish at different ages (and sizes) to the survey. Our basic observation model is

$$I_{s,a,y} \approx Q_{s,a} N_{s,a,y} \exp\{-f_s(M_{s,a} + \delta_{s,y})\},$$

where f_s is the fraction of the year that survey s occurs and the $\exp\{-f_s(M_{s,a} + \delta_{s,y})\}$ term simply projects beginning of year abundance ($N_{s,a,y}$) to the survivors at the time of the survey. We collect all of the M deviations and cohort abundance random effects into the set $\Psi = \{\delta_y, \gamma_c; y = 1,...,Y, c = 1,...,C\}$. Let $q_{s,a} = \log(Q_{s,a}$

) and define $\mu_{s,a,y} = E\{\log(I_{s,a,y})|\Psi\}$ to be the statistical expected value of $\log(I_{s,a,y})$ given all the random effects. The expectations are

$$\mu_{s,a=0,y=c} = q_{s,0}^* + n_{s,0,c} - f_s\delta_{s,c}, \tag{5}$$

and

$$\mu_{s,a,y=c+a} = q_{s,a}^* + n_{s,0,c} - \sum_{i=0}^{a-1}(\delta_{s,c+i} - f_s\delta_{s,c+a}), \quad a > 0, \tag{6}$$

where $q_{s,0}^* = q_{s,0} - f_s M_{s,0}$ and $q_{s,a}^* = q_{s,a} - \sum_{i=0}^{a-1}M_{s,i} - f_s M_{s,a}$. As described in Zhang *et al.* (2020), the $q_{s,a}$ and $M_{s,a}$ values are completely confounded, therefore we cannot directly estimate $M_{s,a}$ without additional information on $q_{s,a}$. As a result, we estimate their combined effect, $q_{s,a}^*$.

The survey index observation equation is

$$\log(I_{s,a,y}) = \mu_{s,a,y} + \tau_{s,y} + \varepsilon_{s,a,y,} \tag{7}$$

where $\tau_{s,y}$ and $\varepsilon_{s,a,c}$ are normally distributed [*i.e.* $\tau_{s,y} \overset{iid}{\sim} N(0, \sigma_{s,\tau}^2)$] survey measurement errors. The random year-effects ($\tau_{s,y}$) allow for measurement errors to be correlated across ages within surveys and years, which is common for survey indices of juvenile ages. However, these errors are independent for different years and surveys. Due to this structure, these year-effects will only affect estimates in a particular year, rather than having a cumulative effect on cohort dynamics like the temporal deviations in M. Furthermore, $q_{s,a=5}^*$ is constrained to be zero for each survey to eliminate the confounding between the values of $q_{s,a}^*$ and $n_{s,0,c}$ in Equation (6). Finally, we estimate between-survey and unstructured correlations in both $M_{s,a,y}$ and $n_{s,0,c}$, which is described in Zhang *et al.* (2020). These correlations represent the metapopulation aspect of the model, where population processes may be similar among NAFO divisions. These correlations were examined with a hierarchical cluster analysis using the `hclust` function in R on the Pearson dissimilarity between surveys.

Data

We used six relative abundance indices of juvenile (ages 1–5) American plaice from stratified random research bottom-trawl surveys in NAFO Divisions 3LNO. These surveys were conducted in the spring (~April–June) and fall (~ October–November) and were separated based on NAFO Divisions (*i.e.* spring 3L, spring 3N, spring, 3O, fall 3L, fall 3N, and fall 3O). We limited the time-series for our analysis to spring surveys conducted after 1996

and fall surveys after 1995 due to low catchability of age 1 American plaice with the bottom trawl gear used in prior years (Morgan *et al.,* 1998). Surveys were not completed in some years and any indices with zero or very small values (*i.e.* $<e^{-5)}$ were not used; see SM. Fig. 1).

Model fitting

We examined thirteen parameterizations of the model, with varying numbers of random effects (γ_c, $\tau_{s,y}$, δ_c) to determine which components were necessary to account for the variability in the sampled survey indices (Table 1). In addition to sequentially adding components, we tested various correlation structures to identify if cohort effects or M deviations varied across space and season. Model selection was completed using a combination of Akaike's information criterion (AIC), Bayesian information criterion (BIC), and examinations of residuals. BIC measures goodness-of-fit, while AIC is a measure of prediction accuracy (Sober, 2002). We used the Template Model Builder (TMB, Kristensen *et al.,* 2016) package in R (R Core Team, 2018) to evaluate the negative logarithms of the marginal likelihoods (nll) of these models and the data, and to evaluate the nll gradients to improve estimation. Further, we used the R function nlminb() to find the maximum likelihood estimates. Model convergence was evaluated by ensuring that the nll gradient for all parameters was $<10^{-4}$ and that the Hessian matrix was positive definite at the maximum-likelihood estimates.

Results

Our model comparisons indicated that the model with the best fit was model M5 which had cohort and year-effects, as well as M deviations that were shared across Divisions (Table 1). Model M5 fit the data well, with no observable trends in residual plots (see SM. Figs. 6–16). This model was an improvement over the simpler model M4, and had no survey year-effects in standardized residuals (SM. Figs. 2 and 3). M4 had clear residual year-effects (SM. Fig. 2) that were substantially reduced in M5, although a similar trend of small magnitude remained (SM. Fig. 3). M5 included spatial and temporal variability in cohort effects (Fig. 2). Despite 3LNO being managed as a single stock, our model selection process showed substantial improvements in estimates when cohort effects were allowed to vary by Division and season (Table 1). The temporal trends indicated that in NAFO Division 3L, cohort effects decreased until 1996, increased after this until 2012, and have since declined somewhat steadily. Meanwhile, there was much less of a trend in NAFO Divisions 3NO, where cohort effects generally oscillated around a mean with a period of around 5–6 years. The similarity in cohort effect trends between 3N and 3O was identified in the spatial cohort effect correlation matrix (Fig. 3) where 3N and 3O surveys always had a high correlation with each another (>0.9). Meanwhile, the correlations between cohort strength derived from 3L surveys and those in 3N and 3O were often lower (≤0.5). This was further illustrated using a cluster analysis that identified that the

Table 1. Model names, descriptions and comparisons using AIC and BIC. + represents effects that were included, while a blank space indicates that the effect was not included. The subscript *d* indicates that the effect was only allowed to vary by Division rather than by survey (*i.e.* season and Division). k is the number of parameters, nll is the negative log-likelihood and the Δ columns represent the difference in the number of criterion points from the model with the lowest respective criterion points. The bolded row (M5) indicates the model that we determined to have the best fit.

| Model	$n_{0,c}$	$n_{s,0,c}$	$\tau_{s,y}$	δ_c	$\delta_{d,c}$	$\delta_{d,c}$ Corr.	$\delta_{s,c}$	$\delta_{s,c}$ Corr.	k	nll	AIC	ΔAIC	BIC	ΔBIC
M1	+								53	834	1773	272	2011	232
M2		+							58	763	1642	141	1902	123
M3		+	+						60	706	1532	31	1801	22
M4		+		+					60	709	1538	37	1807	28
M5		**+**	**+**	**+**					**62**	**689**	**1501**	**0**	**1779**	**0**
M6		+			+				62	714	1551	50	1829	50
M7		+	+		+				64	696	1520	19	1807	28
M8		+			+	+			65	702	1533	32	1825	46
M9		+	+		+	+			67	687	1508	7	1809	30
M10		+					+		65	737	1604	103	1895	116
M11		+	+				+		67	702	1537	36	1838	59
M12		+					+	+	80	692	1544	43	1902	123
M13		+	+				+	+	82	683	1529	28	1897	118
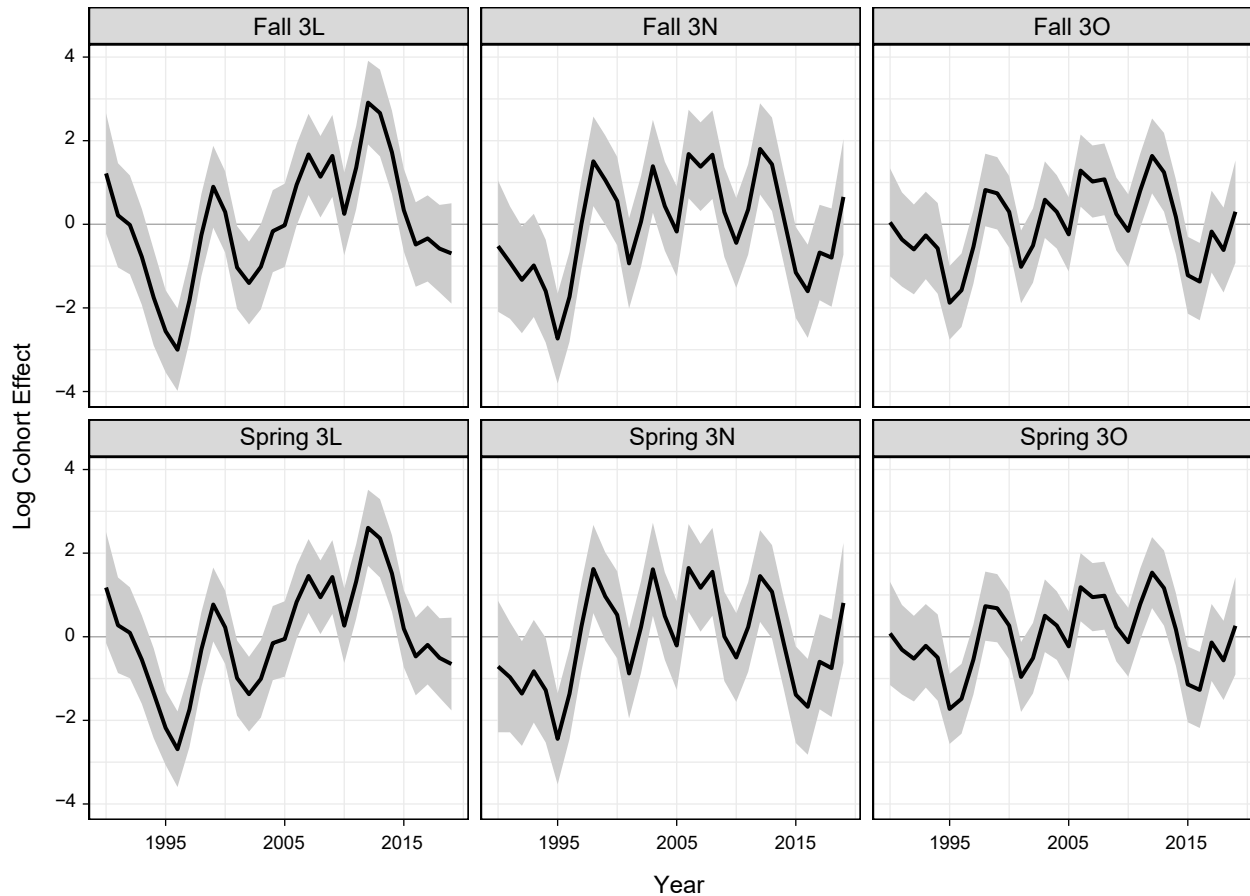
Fig. 2.   Time-series of cohort effect deviations estimated for each survey index using model M5. The black lines represent the point-estimates while the shaded grey area represents the 95% confidence intervals.

cohort effects for 3NO were dissimilar from the cohort effects for 3L (Fig. 4).

Model M5 indicated that accounting for M deviations was necessary to produce the best fits to the survey indices. M5 had the simplest formulation of M deviations, where they were assumed to be equal across NAFO Divisions 3LNO (Table 1). Therefore, unlike cohort effects, our results indicate that M deviations may not vary by Division or season and may be driven by a larger scale process. Finally, despite improving model fit, the estimates of M deviations only differed significantly from zero in four years: 1999, 2005, 2015, and 2016 (Fig. 5). At the extreme, the estimates suggest M's in 2015–16 were slightly more than double those in 1999–2000. Estimated changes in M were much smaller in other years.

Discussion

We applied a state-space metapopulation dynamics model to identify whether American plaice juvenile natural mortality rates (M's) have affected stock dynamics since the population collapse. Our model comparison identified that estimating temporal variability in M improved the model fit to juvenile 3LNO American plaice survey indices which indicates that temporal variability in M may influence the dynamics of the unfished portion of the stock. The best fitting model included spatial cohort and survey year-effects, along with non-spatial M deviations. Although this best fitting model included temporal M deviations, estimates were rarely significantly different from zero. The limited variation in these M deviations in comparison to the larger magnitude variations in age-1 recruitment indicated that juvenile stock dynamics were mainly affected by recruitment. Furthermore, temporal variations in cohort effects were more dissimilar between NAFO Divisions 3L and 3NO, implying that drivers of age-1 recruitment may differ between these regions.

Recent analyses have indicated that current assumptions about M in 3LNO American plaice stock assessments underestimate its impact on the slow recovery for this

stock (Perreault *et al.,* 2020; Wheeland, 2021). Here, we observed that estimating temporal variability in juvenile M improved estimates of juvenile stock dynamics. However, annual M deviations were rarely significantly different from zero, indicating that the variation is less important compared to spatial and temporal variations in cohort strength. This finding matches results from a previous cohort model used for this stock that assessed the potential for changes in M graphically rather than modelling it as we have done here (Kumar *et al.,* 2019). Furthermore, this finding matches broader findings that demersal fish juvenile natural mortality tends to show limited temporal variability (Myers and Cadigan, 1993a; Gudmundsson, 2004). The limited variability in juvenile M may affect our ability to understand the drivers of

current stock assessment problems for this stock. For example, our findings differ from a recent exploration of M deviations where there was an indication that accounting for temporal change in M at young ages would help reduce retrospective patterns (Perreault *et al.,* 2020). This difference in magnitude of influence of natural mortality may have been generated by M deviations at young ages producing better fits by reducing recruitment variance since the Perreault *et al.* (2020) model formulation did not include an M deviation variance penalty like the model employed here. Overall, although increases in M have been suggested by recent studies, we did not find strong evidence for this in juvenile fish.
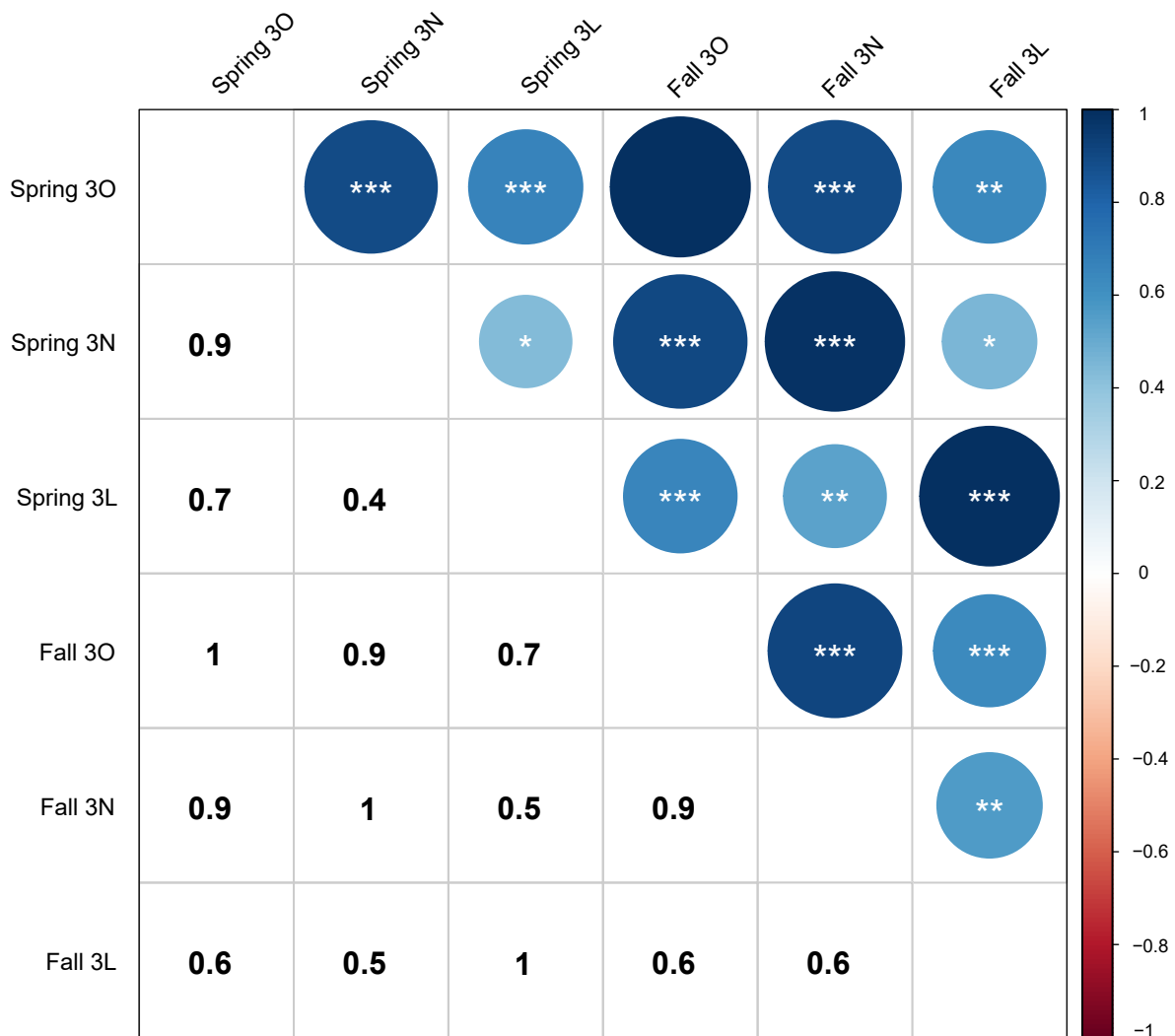

Fig. 3.   Spatial correlations of the cohort effects between the six survey indices from model M5. The size and darkness of the circles indicate the magnitude of the correlations. The stars indicate significance, where more stars represent lower *p*-values (1 star = *P* <0.05, 3 stars = *P* <0.01).

We did not find evidence of large changes in juvenile M since the fishing moratorium in 1995, but this does not mean that high juvenile M is not a factor in the delayed recovery of the stock. It is possible that recent M's are much higher than those prior to 1995. However, our model and the available survey data only allow the estimation of M deviations, which cannot inform the magnitude of M to provide any direct indication of whether current M is high relative to expected levels of juvenile M. As a result, investigating how juvenile M has varied pre- and post-collapse would require a longer historical time series. Since fall survey indices are only available since 1990, they cannot provide much information about pre-collapse M. Spring survey indices go back to 1985, but the survey trawl used in the Spring during 1985–1995 had a larger mesh size than the current trawl and indices for age 1–2 seem less reliable. They include many zeroes that we cannot use in the current model formulation. Although Spring indices at ages 3–5 are more reliable, it would be difficult to differentiate between a change in M and year-effects with survey indices for only three ages. Hence, extending our model back to the mid-1980s does not seem useful. Our juvenile metapopulation dynamics model is only practically useful with indices produced by surveys that are effective at monitoring juveniles, such as the current DFO bottom trawl surveys that use the Campelen trawl.

Unlike the cohort effect, there was little evidence of differences in juvenile M across NAFO Divisions, indicating that the main driver(s) of mortality is likely a large scale process. Large-scale processes affecting juvenile M could include bottom-up processes like bottom-water temperature or prey availability, or top-down processes like predation or competition. Regardless of the particular driver, it is interesting that the spatiotemporal structure of M and age-1 recruitment (*e.g.* cohort effects) differed. Although differences in the spatial scales affecting different aspects of population dynamics are likely inherent in many populations (*i.e.* Levin 1992) recognizing these differences can produce an improved mechanistic understanding of the observed patterns.

The cohort strength effects for juvenile 3LNO American plaice are much larger than the effects of time-varying M. This finding is not particularly novel since understanding recruitment dynamics has been at the core of fisheries science for over a century due to its large influence on population dynamics (*e.g.*, Houde, 2008). However, in a recent analysis of juvenile Atlantic cod dynamics around Newfoundland and Labrador, oscillations with a similar period to those estimated here were identified in both M deviations and cohort effects (Zhang *et al.*, 2020). Furthermore, these oscillations are similar to estimates of weight-at-length (an indicator of condition and potentially

starvation induced mortality) for 3Ps Atlantic cod (Cadigan *et al.,* 2022). The 3Ps Atlantic cod model estimates were compared to regional drivers and significant correlations were identified for oceanographic (*e.g.* bottom water temperature), basal food web (*e.g.* zooplankton), and direct prey abundance (3LNO Northern sand lance (*Ammodytes dubius*)). Therefore, it is possible that Atlantic cod and American plaice recruitment and/or M are affected by similar environmental and/or trophic mechanisms.

In addition to the influence of age-1 recruitment, we also observed a substantial influence of survey year-effects on model estimates. Survey year-effects are used to account for correlated observation error among ages in a particular survey that can occur for a variety of unknown reasons (Myers and Cadigan, 1995). For example, catchability may vary annually depending on environmental conditions, there may be anomalous sets accounting for a majority of catch, or there could be differences in how survey crew handles the fishing gear. Additionally, the survey year-effects may be necessary to account for stock distributional shifts (Swain and Sinclair, 1994; Swain and Benoit, 2003). Accounting for these year-effects is important when modelling juvenile dynamics based on survey indices; however, their source(s) remains speculative.

There is substantial evidence that M varies with body size and age, often by orders of magnitude over the life cycle (Lorenzen *et al.,* 2022). Although our metapopulation dynamics model was based on separate age-dependent M's for each metapopulation, we assumed that annual deviations in M were the same for all ages even though the absolute value of M could differ substantially among ages. Yet, this simplifying assumption may be unrealistic. For example, if M at age 1 is 2.0 and M at age 5 is 0.3 then it is possible that annual M deviations at age two are larger than at age five. However, additive M deviations have a multiplicative effect on cohort survival; that is, if $M_{a,y} = M_a + \delta_y$ then $N_{a+1,y+1} = N_{a-1,y-1}\exp(-M_a)\exp(-\delta_{y-1})$. If annual M deviations are multiplicative in nature then a more realistic M model would be $M_{a,y} = M_a\exp(\delta_y)$ or $\log(M_{a,y}) = \log(M_a) + \delta_y$ (Cadigan, 2015; Stock and Miller, 2021). Using the approximation $\exp(\delta_y) \approx 1 + \delta_y$, then $M_{a,y} = M_a\exp(\delta_y) \approx M_a + M_a\delta_y$. Note that if δ_y is normally distributed with mean zero and stationary variance $\sigma_\delta^2/(1 - \varphi_\delta^2)$ then $M_a\delta_y$ also is also normally distributed with mean zero but with stationary variance $M_a^2\sigma_\delta^2/(1 - \varphi_\delta^2)$. As a result, the necessity for using multiplicative rather than additive M deviations for a population where M_a decreases with age could be explored by examining whether there is higher residual variation at younger ages in an additive M deviation model. This is exactly the pattern we found (see SM. Fig. 4). However, it is also possible that the $\varepsilon_{s,a,c}$ survey measurement error variances (see Equation 7)
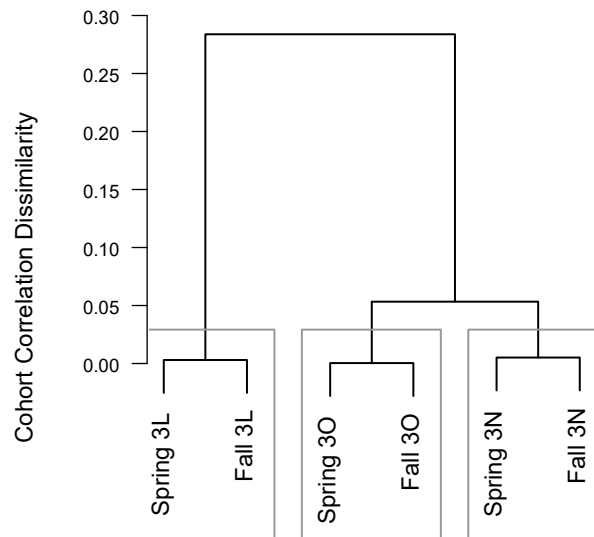
Fig. 4. Dendrogram of a dissimilarity matrix of the spatial correlations of cohort effects in model M5.

are higher at younger ages, which is another possible model misspecification. The within-survey variance of the indices may indicate if the patterns in SM. Fig. 4 are consistent with sampling variability or not, but these sampling variances were not available to us. Therefore, given the current data, these effects are confounded and we cannot identify whether the observed residual variance pattern is the result of process or observation error. Finally, implementing a model with multiplicative M deviations would also require that we specify the age pattern in M's. However, we are unsure why the residual variation in SM. Fig. 4 usually increases at age five but sometimes at age four. These are areas that require further research.

We identified that the recruitment trends appear to differ between NAFO Divisions 3L and 3NO despite these management Divisions comprising the same stock. Similar results were found in a different cohort model used for American plaice stocks throughout all of Newfoundland and Labrador (NAFO Divisions 2J3KLNOPs; Kumar *et al.*, 2019). The spatial extent of management on the Grand Bank varies by species. Yellowtail flounder and American plaice are the only two species whose management occurs across NAFO Divisions 3LNO, whereas other species are managed separately between 3L and 3NO
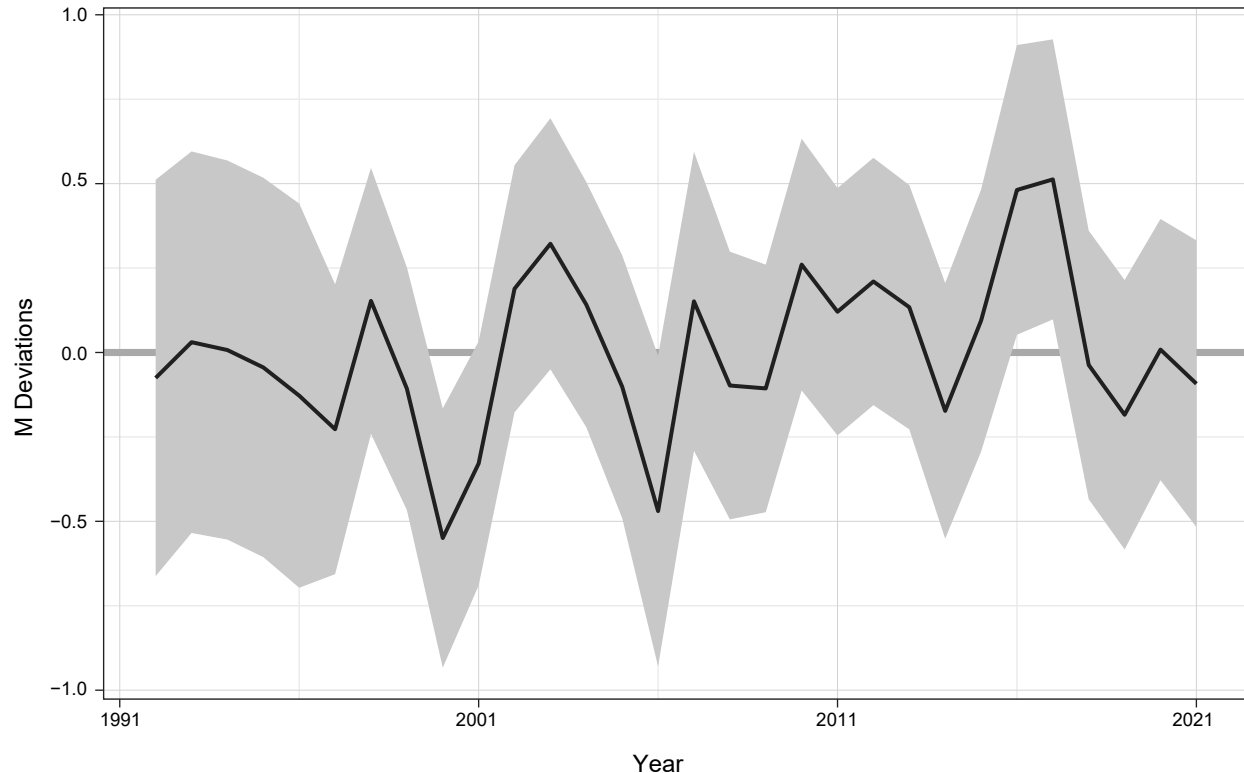

Fig. 5 Time-series of annual natural mortality rate deviations from model M5. The black line represents the point-estimates and the shaded grey area represents 95% confidence intervals.

(*e.g.* 2J3KL vs. 3NO Atlantic cod). Previous studies have argued that American plaice in NAFO Division 3L differ from those in 3NO (see review by Brodie, 2002). These arguments have stemmed from various lines of evidence including differences in growth and maturity (Zheng *et al.*, 2020b), in divisional research surveys indicating different trends in abundance, and as a result of the general sedentary nature of American plaice in this region (Pitt,1969; Morgan, 1996). Since incorrect delineation of stock spatial structure can affect estimates of productivity and in turn affect management decision-making (*e.g.* Kerr *et al.,* 2017), further work on addressing this question for 3LNO American plaice is warranted.

Acknowledgements

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